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ECOLOGY OF THE WILLOW CONE GALL.

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AMONG the numerous galls to be found everywhere, the cone galls of the willows are very common forms. A little has been done toward their knowledge by Walsh, who has dealt more particularly with descriptions of the galls and their makers and has done little more than make casual mention of ecological relations. An examination of the galls in fall or winter shows them to be the abiding place of the larvæ of a goodly number of insects. Walsh says: "Nothing gives us a better idea of the prodigious exuberance of insect life, and of the manner in which one insect is often dependent upon another for its very existence, than to count up the species which haunt, either habitually or occasionally, one of these willow-galls, and live either upon the substance of the gall itself or upon the bodies of other insects that live upon the substance of the gall."

In the following pages will be discussed, first, the galls themselves, second, the gall makers, and third, the guests and parasites that inhabit the galls.

THE CONE GALLS.

As is well known, a gall is some abnormal growth of a plant tissue resulting from an external stimulus. In the case of the cone galls and of the other bud galls of the willow the stimulus is furnished by the gall gnat. Whether it is given by the insertion of the ovipositor into the bud, by the presence of the egg, or by the larvæ, I cannot say. The gall attains its full growth by midsummer thus giving evidence of considerable stimulation. Regularity and symmetry in the shape of the gall can be accounted for by the stimulus, whatever it may be, acting equally in every direction.

As a result of this stimulus, the bud takes on a remarkable



a b c d e f

FIG. 1.—Cone gall of *Salix*. a, b, c, *Salix gnaphaloides* (showing variation in crook of stem); d, *Salix strobiliscus*; e, f, *Salix strobiloides*.

activity in growth, and develops a large number (60-75) of scales. These scales are placed in regular order, with their edges overlapping, and form in the center an elongate cell. This cell, protected by the numerous layers of scales, is the abiding place of the gall maker during its larval and pupal stages.

The three cone galls on which I have based most of my study are all found in the vicinity of Lake Forest, Illinois. I also gathered some material in southwestern Wisconsin. They are formed from apical buds. In structure and appearance they are much alike but they have some characteristic differences. The three are:—

1. A pubescent gall found growing on *Salix cordata* Muhl., which corresponds in every particular to the gall found by Walsh on the same willow. This is the gall *Salicis strobiloides* O. S. (Fig. 1, *e* and *f*). It is usually somewhat spherical but occasional galls have the central scales prolonged into a loose tip. It is the dense silvery pubescence which distinguishes this gall most clearly from the others.

2. A cone gall usually more tapering than the above and lacking the dense pubescence. Its marked characteristic is a decided curve or bend in the twig just beneath the gall (Fig. 1, *a, b, c*). In every respect the gall corresponds to *Salicis gnaphaloides* Walsh, but in no case have I found it on *Salix humilis*, the willow to which Walsh accredits it. Instead, I have found it in great abundance on *Salix bebbiana*.

3. A gall corresponding exactly to *Salicis gnaphaloides*, except that the twig is straight (Fig. 1, *d*), was also found on *Salix bebbiana*, the *Salix rostrata* of Walsh's paper. These galls were not in such great abundance and were usually to be found on the same plant with the gall *S. gnaphaloides*. In some two or three cases small shrubs bearing only a few galls had all straight-stemmed ones. On one shrub with 37 galls, 9 were straight and 28 were crooked. From another clump of willows (*S. bebbiana*) I gathered 65 galls, of which 57 were crooked and only 8 straight. In both cases there was a gradation in the matter of the crook.

Since I shall show a little farther on that these three galls have the same maker, it is evident that the distinction between the first and the others may be due to the peculiar reactions of the different willows to the stimulus which causes the growth of the gall. But in the case of the two galls on *S. bebbiana* the cause of the difference does not seem so clear. It will be necessary to observe the beginning of the gall to see if this can be determined.

In his *Origin of Floral Structures*, Henslow has drawn an analogy between the gall and the flower. He intimates that the gall is the result of the shortening of the axis due to puncturing in the depositing of eggs by insects, and thus represents a lessened growth of twig. I believe that the gall does not represent a shortening of the axis, but, on the other hand, represents a special growth of scales in addition to the normal growth of twig. I base my belief on the following observations:—

1. The scales of the gall have not the normal leaf arrangement or venation. From a single clump of willows (*S. bebbiana*) I gathered a number of twigs and galls. The lateral buds of this willow have the two fifths arrangement. If the gall represents a shortening of the axis the scales ought to show some such arrangement, allowing for a reasonable amount of displacement owing to crowding. While the general arrangement of the scales was in whorls, some showed a spiral arrangement but never the two fifths. I examined in detail about a dozen galls to determine this. Moreover the scales do not very much resemble the leaves of the willows. They differ in shape and margin and show little or no venation and never the venation of the leaf.

2. The gall-bearing shoot is oftenest longer than the non-gall-bearing and develops more lateral buds. From this same bunch of twigs I took 28 bearing the crooked galls and the same number of non-gall-bearing twigs. The average number of lateral buds to the gall-bearing twigs was 20, while the average to the non-gall-bearing twigs was only $16\frac{1}{4}$. Eleven gall-bearing and ten non-gall-bearing twigs were taken from the same part of the plant, having had, as nearly as could be determined, the same conditions of growth. The former had an average of $17\frac{1}{11}$ lateral buds and an average length, from origin of the twig to the base of the gall, of 6.84 inches, and the latter had an average of 17 lateral buds and an average length to base of terminal bud of 6.825 inches. In every case the twigs were of 1904 growth. General observations of various clumps of willows confirmed the foregoing results. However, in one case the average length of five pubescent gall twigs (*Salix cordata*) was 1.13 inches less than the average length of seven non-gall-bearing

ing twigs growing under similar conditions. The former averaged three more lateral buds to a twig than the latter. From another clump of willows 14 twigs bearing pubescent galls had an average of three buds fewer than 14 non-gall-bearing twigs (15 and 18) but the average length was equal.

I conclude that the gall does not represent a shortening of the axis and that the gall-bearing twig does not represent a lessened growth, but that, on the other hand, the gall-bearing

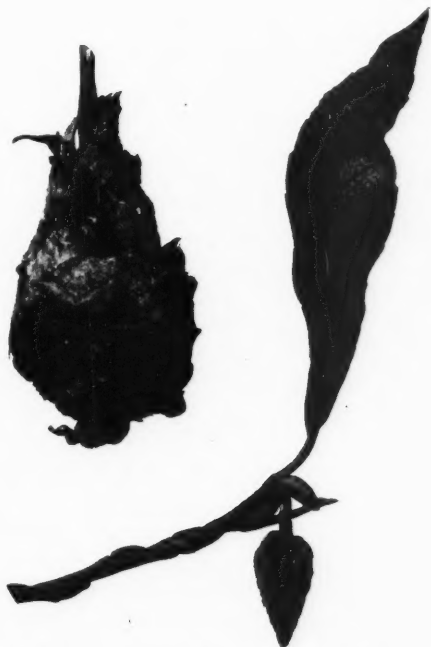


FIG. 2.—Two cone galls showing extremes in size. The larger shows protruding pupal skins of the moth *Acleris*. At the base of the crooked stem of the smaller is a bud favorably placed for continuing growth in a direct line.

twig holds its own with the non-gall-bearing and has in addition the abnormal growth of the gall.

The very abnormal shape of the stem of the crooked gall suggests a question as to its purpose. Since the gall terminates the twig and prevents further apical growth, future growth must

be by means of a branch originating on the twig below the gall. At first it appears as if the crook in the stem (see Fig. 2) might provide for a direct growth by means of a branch from the convex side of the stem. Dr. P. Speiser claims that a bend in the stem is of advantage in this way in the gall *Dichelomyia rosaria* H. Lw., since the gall is turned aside, and thus permits a more or less direct growth from a bud below it. An examination of any willow bearing these crooked galls (*S. gnaphaloides*) shows very plainly that the benefit for continued growth is accidental rather than habitual. To be of service it would be necessary that a bud be located just at the beginning of the crook in the stem. In one lot of 57 galls, 32 had buds so located and 25 were without bud in a favorable position. By watching the willows for further information, I found that very frequently the favorably placed bud either does not develop or sends off a branch at an angle from the parent twig. And just as frequently, when there is no bud so favorably located, a bud farther down, or one immediately beneath the gall, is the one which sends out the most vigorous branch, whose direction is determined by its surroundings.

THE GALL MAKERS.

The life history of the gall gnat is very simple. In the spring the larva which has spent the winter in its cell in the gall transforms into the pupa and that, a little later, into the gall gnat itself. The gnats soon deposit their eggs in apical buds of willows. From the eggs larvæ are hatched and the cycle begins again. Walsh speaks of observing larvæ as late as April 23, and pupæ from early in April until late in May. From galls gathered and examined on the following dates I found larvæ of the gall gnats: October, November 12, December 26, January 17, February, about March 20, and the first and second weeks of April. In March and April, many larvæ were almost ready for transforming into pupæ but only a few pupæ were found. Gnats had emerged from all the galls examined June 3. I kept some of the galls gathered in December and on subsequent dates, to watch for transformations. From those of December 26, one or

two gnats emerged about the middle of February. From those of March 20 several gnats emerged early in April. From the April specimens they began to appear within a week and continued to emerge for over three weeks. Because of the difficulty in rearing gall gnats my data are not complete. But it is evident that the insect exists for a long time in the larval state and that the pupal period is comparatively short.

Walsh found it difficult to devise an artificial mode of treatment for rearing the gall gnats in the house. My results with



FIG. 3.—Gall gnat (*Rhabdophaga strobiloides* O. S.) enlarged.

the earlier lots of galls were not very successful. At first I threw them in jars and boxes but found that in a short time larvæ and pupæ dried up in many of the galls. Then I tried keeping them with the stems in water but with scarcely better success. With the last lot I used a different plan. I tied the galls in squares of cheese cloth, opening the bundles and sprinkling them every day or two. This plan was very successful. Of course it is possible that the season had something to do with it, for it was nearly the regular time for the emerging of the gnats. But that cannot be the full explanation, for, in packages which were neglected, the results were less satisfactory. The sprinkling seems to have taken the place of the spring showers.

Cecidomyiids offer considerable difficulty in the matter of

specific determination. Walsh has called the maker of each of the fifteen willow galls he describes a distinct species. If the galls themselves could be taken as a means of determining species his results would in most cases stand. Although I have been working with only a few of the cone galls, it is necessary to consider some others in settling this question.

Of Walsh's fifteen willow galls, six are more or less cone-shaped bud galls of somewhat similar structure. The larvæ found and described by Walsh in these six are precisely alike as to size, shape, "breast bone," etc. Walsh gives, however, the following differences in the cocoons:—

Cecidomyia salicis brassicoides, cocoon scarcely larger than larva.

Cecidomyia salicis strobiliscus, cocoon $1\frac{1}{2}$ to 2 times as long as larva.

Cecidomyia salicis gnaphaloides, cocoon $1\frac{1}{2}$ to 2 times as long as larva.

Cecidomyia salicis coryloides, cocoon 2 times as long as larva.

Cecidomyia salicis strobiloides, cocoon $2\frac{1}{2}$ to 3 times as long as larva.

Cecidomyia salicis rhodoides, cocoon $2\frac{1}{2}$ to 3 times as long as larva.

The difference seems to be considerable but it is easily explained. I have examined all except the fourth (*coryloides*), ten or more galls of each, and have found the length of the cocoons to vary in the different galls in proportion to the length of the central cell or cavity (see Fig. 5). The gall *S. brassicoides* has a short cell which permits of only a short cocoon, while the gall *S. strobiloides* has a long central cell giving plenty of space for a long cocoon. If the cocoon is exuded from the larva and is expanded by a gas, as Walsh supposed, then the length and size of the central cell certainly would determine the size of the cocoon.

In these same six species Walsh found the pupæ of only five. The only difference I can find in his descriptions is that *C. s. gnaphaloides* (in dried specimens) is slightly shorter than the others. I could not find this difference.

From a careful comparison of Walsh's descriptions and from

verifications by observation in the case of the cocoons of five of the galls and in the case of the larvæ and pupæ of three of them, I am convinced that specific differences, if any, must be looked for in the imagoes, for they cannot be found in the earlier stages.

Imagoes of the makers of five bud galls were found and described by Walsh. I give below a table showing the differences which he finds in them.

Imagoes of Bud Gall Makers.

Species	<i>brassicoides</i>	<i>strobiloides</i>	<i>strobiliscus</i>	<i>gnaphaloides</i>	<i>rhodoides</i>
Antennal Joints	22-24	21-22	23-24		21-25
Thoracic Hairs	Dusky	Whitish	Whitish	Whitish	Whitish
Length in Inches	0.16-0.20	0.16-0.20	0.16-0.20	0.12-0.15	0.16-0.20
Origin of Anterior Branch of Cubital Wing Vein	Occasionally obsolete	Always obsolete for a short space	Rather distinct	Rather distinct	Occasionally obsolete

The variation in the number of antennal joints makes that feature useless as a specific characteristic. Antennæ of dried specimens are easily broken, but by using fresh and alcoholic specimens, I find that there are about the same number of joints in those of all the gnats which make the different galls.

The color of thoracic hairs is the first and only distinguishing characteristic. I have had only five imagoes of *C. s. brassicoides* Walsh but find that the dusky hairs are present in all, while in the gnats from the four other galls the thoracic hairs are whitish.

Length shows no difference except in the one case, and I think this cannot be considered for I found four, from one lot of five imagoes from the gall *S. gnaphaloides*, which were fully 0.21 inches in length, and I have found but one or two as short as 0.12 inches.

As to wing venation the wings of four *C. s. brassicoides* Walsh have the origin of the anterior branch of the cubital vein distinct. Seventeen left and eighteen right wings of *C. s. strobiloides* Walsh gave the following results as to the origin of the anterior branch of the cubital vein:—

Origin of 16 anterior veins obsolete.

Origin of 6 anterior veins very indistinct, probably obsolete.

Origin of 4 anterior veins indistinct, probably not obsolete.

Origin of 9 anterior veins distinct.

These results do not agree with Walsh's statement but, on the contrary, show that this feature of the wing venation cannot be taken as a specific characteristic. Wings of five *C. s. gnaphaloides* Walsh and two *C. s. strobiliscus* Walsh have the

origin of the anterior branch very distinct. Four *C. s. rhodoides* Walsh show it "occasionally obsolete" as given by Walsh. The fact that variations do occur and that each of the so called species has some individuals with the venation like that of other species is sufficient to throw this out as a determining characteristic. Walsh says him-

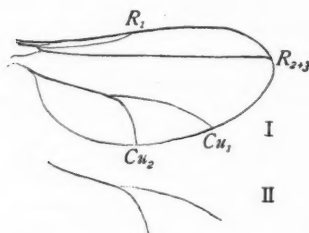


FIG. 4.—Wing venation of gall gnat. Cu_1 , Anterior branch of cubitus. I. Origin distinct II. Origin obsolete.

self that the imagoes of his *gnaphaloides* and *rhodoides* are indistinguishable except for size, and I have shown that this difference is not fixed.

His *brassicoides* differs from the others in having dusky instead of whitish thoracic hairs. Since the few specimens I have had showed this same difference, it is necessary, at least until other material is available, to let *C. brassicoides* stand as a distinct species. But from the data I have given and from the comparison I have made of Walsh's descriptions with each other and with my specimens, I must conclude that *strobiloides*, *strobiliscus*, *gnaphaloides*, and *rhodoides* are synonymous. Since the first name was given by Osten Sacken in 1861, I have taken it as the name of the species and the three others as synonyms. So the gnat which produces the four galls, *Salicis strobiloides*, *Salicis strobiliscus*, *Salicis gnaphaloides*, and *Salicis rhodoides* is *Rhabdophaga strobiloides* O. S. This verifies the inference of Bergenstamm and Löw that Walsh's species are all *strobiloides*.

Summarizing, *Rhabdophaga strobiloides* O. S. produces: gall

Salicis strobiloides on *Salix cordata*; gall *Salicis strobiliscus* on *Salix bebbiana*; gall *Salicis gnaphaloides* on *Salix bebbiana*; gall *Salicis rhodoides* on *Salix humilis*.

GUESTS AND PARASITES.

While I was gathering material for the study of the gall gnat I bred as many as possible of the other insects which inhabit the galls. These include not only the inquilines and the transient guests, but also a number of parasites which live on these inquilines or on the gall maker.

In making my table of results I have included a few species bred by Professor J. G. Needham from cone galls and from the galls *S. rhodoides* and *S. brassicoides* during the spring of 1904.

List of Insects bred from Galls.

	Gall <i>S. strobiloides</i>	Gall <i>S. gnaphaloides</i>	Gall <i>S. strobiliscus</i>	Gall <i>S. rhodoides</i>	Gall <i>S. brassicoides</i>
Gall makers:					
<i>Rhabdophaga strobiloides</i> O. S.	×	×	×	×	
<i>Rhabdophaga brassicoides</i> Walsh					×
Inquilines:					
<i>Cecidomyia albovittata</i> Walsh	×	×	×		
<i>Chaitophorus</i> sp. (plant louse)	×	×	×		
<i>Pontania pisum</i> Walsh (saw fly)	×	×	×		
<i>Euura noda</i> Walsh (saw fly)	×	×	×		
<i>Xiphidium ensiferum</i> , eggs (meadow grasshopper)	×	×	×		
A spring-tail (<i>Thysanura</i>)	×	×	×		
<i>Acleris heindelana</i> Fernald (a moth)		×	×		
Larvæ of a Noctuid (<i>Lepidoptera</i>)			×		
Larva of Tineid (?) (<i>Lepidoptera</i>)		×			
Larva of <i>Thyridopteryx ephemeraformis</i> (?) (<i>Lepidoptera</i>)		×			
Parasites and hyperparasites:					
<i>Tetrastichus</i> sp.	×	×			×
<i>Tetrastichus</i> sp.	×	×			×
<i>Tetrastichus</i> sp.	×				×
<i>Polygnotus salicicola</i> Ashm. (a Proctotrupid)	×	×			×
<i>Eurytoma studiosa</i> Say (a Chalcid)	×	×			×
<i>Pteromalus</i> sp. (a Chalcid)	×		×		
<i>Torymus popenoi</i> Ashm. (a Chalcid)	×				×
<i>Aphanogmus virginianensis</i> Ashm.	×	×			

Lists of Insects bred from Galls. (Continued.)

	Gall <i>S. strobiloides</i>	Gall <i>S. gnaphaloides</i>	Gall <i>S. str-obliticus</i>	Gall <i>S. rhodoides</i>	Gall <i>S. brassicoides</i>
<i>Aphelinus mytilaspidus</i> Le Baron (a scale parasite)		×		×	
A Campoplegine	×				
An Encyrtine	×				
<i>Copidosoma intermedium</i> How.	×				×
<i>Urogaster forbesii</i> Ashm.	×				×
<i>Tridymus metallicus</i> Ashm.		×			×
<i>Dapanus</i> n. sp. (an Ichneumonid)	×				
<i>Oncophanes</i> n. sp. (a Braconid)	×				
Transient and accidental guests:					
<i>Megalothrips</i> sp.	×				
<i>Phlaothrips</i> sp.	×				
<i>Ischnorhynchus reseda</i> Panzer (Heteroptera)	×				
<i>Triphleps insidiosus</i> Say (Heteroptera)		×			
A pseudoscorpion		×			

Thus we find at least 32 species of insects making use of the cone galls. Of these, one is a gall maker, 10 areinquilines, 16 are parasites or hyperparasites, and 5 are transient or accidental guests. It will be noticed that the greater number are from *S. strobiloides*, which may be due to the better protection offered by the dense pubescence. The larger insects were more numerous than small ones in *S. gnaphaloides*.

The following description of the moth bred from the gall *S. gnaphaloides* has been furnished for publication in this paper by Professor C. H. Fernald:—

***Acleris heindelana* Fernald n. sp.**

Expanse of wings, 15–17 mm. Head, thorax, and fore wings dull steel gray, the wings with a trace of light brown stain below the large triangular dark brown costal spot which extends from the basal third to near the outer fifth of the costa and about halfway across the wing. This spot has minute scattered tufts of blackish scales over the surface and there are also a few other blackish scale tufts in places common to the species of this genus.

Fringes concolorous with the adjoining surface of the wing. Hind wings pale gray with a silky luster, a little darker at the apex, and with the fringes of the same color as the base of the wings. Under side of the fore wings much darker than the hind wings and with the costa marked alternately with light and dark gray. The hind wings are sprinkled with brown dots towards the apex. Abdomen of the same color as the hind wings.

Described from two female specimens: one from Lake Forest, Ill., and one belonging to the U. S. National Museum and taken in Winnipeg, Manitoba, by A. W. Hanham.

I have one specimen in rather poor condition which may possibly belong to this species. It is labeled as follows: "Ft. Klamath, Ore., 10.6. '86. T. C. M. Coll."

Eggs of the meadow grasshopper (*Xiphidium ensiferum*) were found in both old and recent galls. In many cases they were dried up. The grasshoppers began to appear in May. Wheeler says that the meadow grasshoppers seem to prefer the blackened and weatherbeaten galls, probably because their scales are more easily forced apart. He believes that this insect's habit of putting its eggs in the galls is of comparatively recent acquisition because in some cases the eggs are poorly placed and because the insect still uses galls whose scales are so close together as to flatten and kill the eggs, evidence that the grasshopper has not learned to distinguish the kind of gall best adapted to its purpose. If we accept Wheeler's conclusion, we may say that the gall is of increasing importance to the insect world.

So far as is known, *Tetrastichus* is hyperparasitic. There are numerous undescribed species which are difficult to separate.

Polygnotus salicicola was bred from a Cecidomyiid leaf gall of the willow by Mr. A. Koebele at Los Angeles, Cal.

Mr. Theo. Pergande says that both of the thrips, *Megalothrips* and *Phlæothrips*, are apparently undescribed.

Ischnorhynchus resedæ Panzer is a common European species, also common in the United States. *Triphleps insidiosus* Say is a common and widespread species found upon berries and upon the ox-eye daisy.

Although it is difficult and often impossible to identify the various insects in their larval state, still an early examination is of value for showing the abundance of life in the individual galls. Usually the larva of the gall gnat which is the maker of the gall,

is present in its central cell. It is easily recognized, not only by its larger size, but especially by the presence of the "breast bone" so characteristic of all Cecidomyiid larvæ. Larvæ of small Cecidomyidæ are found in considerable numbers between the outer scales of many galls.

These are also recognized by the "breast bone" but with greater difficulty because of their smaller size.

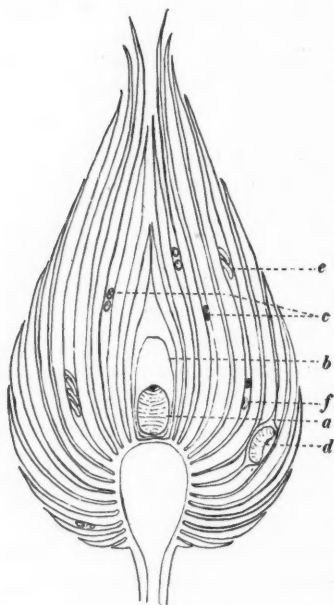
Twenty-three 1904 pubescent galls from the region of Pettibone Creek, north of Lake Bluff, Ill., gathered and examined in October, 1904, contained fifteen living and two dead larvæ of the gall gnat which produces the gall (6 galls were without *Rhabdophaga* larvæ), 169 small Cecidomyiid guest larvæ, 6 larvæ of Hymenopterous parasites of which two were in the central cell of one gall in place of the *Rhabdophaga* larva, and 384 meadow grasshopper eggs. One 1903 gall from the same place contained 16 grasshopper eggs.

Nine 1904 pubescent galls from South Wayne, Wis., gathered December 26, 1904, contained 9 larvæ of gall

FIG. 5.—Diagrammatic drawing of section of a cone gall, showing positions of gall makers and others. *a*, *Rhabdophaga* larva; *b*, its cocoon; *c*, guest Cecidomyiid larvæ; *d*, saw fly or moth larva in a burrow; *e*, eggs of *Xiphidium ensiferum*; *f*, larva of Hymenopterous parasite.

gnats, 1 guest Cecidomyiid about half as long as the gall maker, 37 smaller Cecidomyiid larvæ, 2 parasitic larvæ, and 13 grasshopper eggs. Six 1903 galls from same place contained 32 grasshopper eggs.

Seventeen 1904 crooked-stem galls from west of Lake Bluff Ill., gathered January 17, 1905, contained ten larvæ of the gall maker, 28 Cecidomyiid larvæ about half as large as maker, 10



smaller Cecidomyiid larvæ, 5 saw fly larvæ, 13 larvæ of Hymenopterous parasites, and nearly 400 grasshopper eggs. Three 1903 galls from same place contained 3 saw fly larvæ and about 125 grasshopper eggs.

I can conclude with no more appropriate words than those which Walsh used in connection with another gall: "If this one little gall and the insect which produces it were swept out of existence, how the whole world of insects would be convulsed as by an earthquake! How many species would be compelled to resort for food to other sources, thereby grievously disarranging the due balance of insect life! How many would probably perish from off the face of the earth, or be greatly reduced in numbers! Yet to the eye of the common observer this gall is nothing but an unmeaning mass of leaves, of the origin and history of which he knows nothing and cares nothing!"

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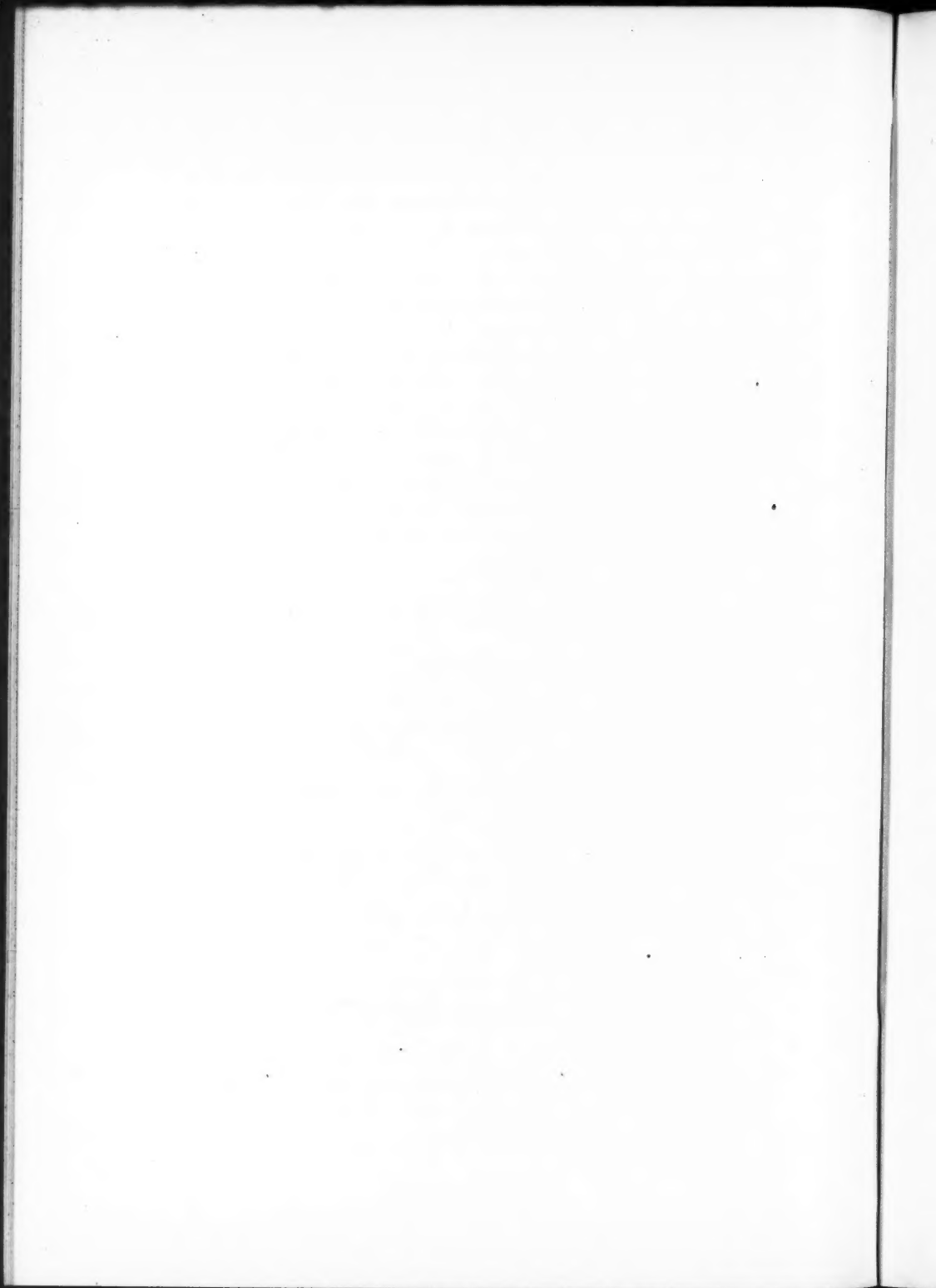
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FOREST CENTERS OF EASTERN AMERICA.

EDGAR N. TRANSEAU.

AN examination into the distribution of the forest trees of eastern North America develops the fact that there are several natural vegetation centers. Adams (:02) called attention to the

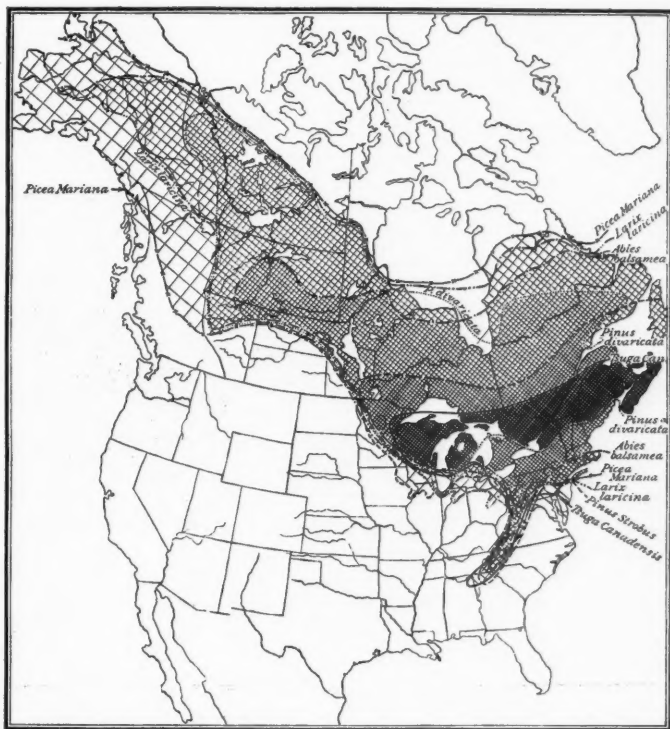


FIG. 1.—Map showing distribution of several of the dominant Conifers of the Northeastern Conifer center. The relative intensity of shading indicates the relative number of species found in the region.

distinctness of the biota of northeastern and of southeastern America, and showed that they are to be regarded as centers of

dispersal for the fauna and flora. In a former paper the writer (:03) pointed out that if the distribution of the characteristic bog plants be plotted on a map, the Laurentian region of Canada is indicated as their center of distribution. Within its limits, the plants have a wider range of habitats, attain a greater size, and are more abundant than elsewhere. It is also shown that



FIG. 2.—Map showing distribution of *Picea canadensis*, *Acer pennsylvanicum*, *Betula papyrifera*, *Prunus pennsylvanica*, and *Betula lutea* about the Northeastern Conifer forest center. The writer is under obligations to Professor Aven Nelson, Dr. P. A. Rydberg, and Mr. W. P. Holt for unpublished data which aided in the construction of this map.

the tree species are most limited in extent of dispersal, the bog shrubs have a wider range, while the herbaceous plants range from the Arctic seas to the Gulf of Mexico.

In using the term "center of distribution" it is not implied that the plants have necessarily spread from these centers, but that the complex of climatic factors most favorable to the development of this type of vegetation is here localized, and that as we depart from such centers we find conditions more and more unfavorable. This implies the elimination of such species as are most rigidly dependent upon definite conditions. Compare for example (Fig. 1) the distribution of *Pinus strobus* and *Tsuga canadensis* with that of *Picea mariana* or *Larix laricina* and note the intermediate dispersal of *Abies balsamea*. Fig. 2 shows the distribution of several other species and still further reinforces the suggestion that the St. Lawrence basin is a definite center about which is distributed a unique type of forest. It is floristically related to the forests of other parts of the continent but ecologically and climatically it is distinct.

The recognition and separation of these centers is of the greatest importance at the present time when there is so much activity along physiographic ecological lines. That there is a natural succession of plant societies in a given locality has long been recognized. Cowles (1911) has shown that this succession may be correlated with the physiographic development of the region, because soil structure, water content, and slope are largely determined by it. Already the applicability of this hypothesis has been demonstrated in many parts of the United States.

But thus far little attention has been paid to the relation which the successive plant societies found in an area bear to their centers of distribution. In other words, the societies have been studied from their physiographic, but not from their geographic aspect. Such a geographic outlook, however, not only aids in the selection of the characteristic plants of the local habitat, but also throws light on the relative importance of the several societies. The geographic point of view is also necessary to furnish a suitable basis for comparing local meteorological data. Unless the climatic conditions of the centers of distribution of the societies are pointed out, the meaning of local climatic data is not apparent. Further, it is probable that in many areas the societies are not all members of the same geographic center,

so that comparisons with the conditions in two or more centers may be necessary to interpret fully the local data.

The geographic point of view is of the greatest importance in the study of regions intermediate between the great plant formations. In such localities there is a mingling of both species and societies which have spread from very different distribution centers. The local order of succession is usually a mixture of two or more orders, characteristic of as many centers. For example, in northern Michigan the successive societies (Whitford, :01) in the development of the forests, are: (1) xerophilous herbs, (2) the heath, (3) the coniferous forest, and (4) the maple-beech climax forest. While there can be little doubt but that this is the correct interpretation of the forest relationships in this region, there is a notable difference between these societies. The first three may be found anywhere in that region, while the last occurs only in areas favored by a rich soil, the climatic influence of the lakes, and the possibilities of migration from the southeastern deciduous forest. The first three societies are stages in the development of the climax forest of the Northeastern Conifer forest center, the last is the attenuated border of the climax stage of the southeastern Deciduous forest center. The first three stages are largely physiographic, while the last is also geographic, for it marks not only the succession of one society over another, but also the invasion and succession of one forest center over another.

In northern Pennsylvania and part of the mountains of New England, it appears from preliminary work that the successional relationship of the societies can only be traced by taking into account the fact that the societies of northern slopes and certain other edaphic situations are related to the Northeastern Conifer forest and form an order of succession *distinct* from that to which the societies of southern slopes and other favored situations belong.

Where best developed in the lower Ohio basin and Piedmont plateau, the climax stage of the Deciduous forest center (Fig. 3) is made up of many species of which the dominant are *Quercus alba*, *Magnolia acuminata*, *Acer saccharum*, *Fagus americana*, *Liriodendron tulipifera*, *Fraxinus americana*, *Quercus rubra*, and

Hicoria alba. Of these species the most hardy are the beech and the maple. In many places in the northern states the latter occupies areas almost to the exclusion of other trees, while within the southeastern center it is only one of many species in

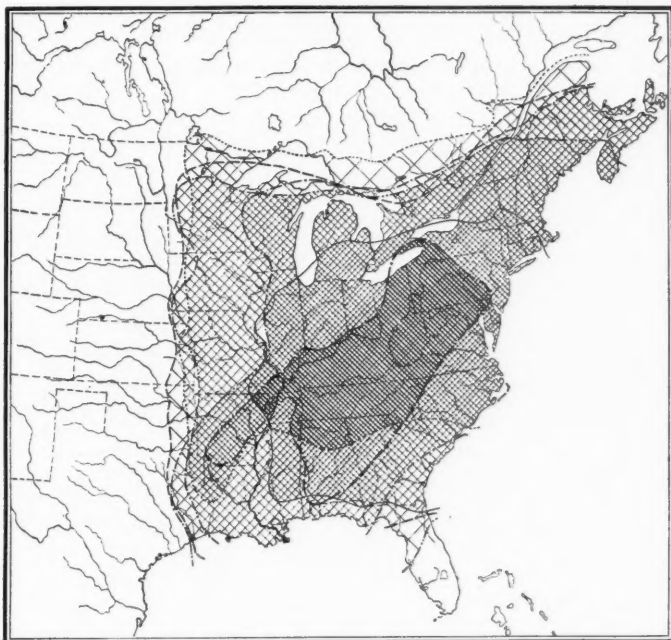


FIG. 3.—Map showing distribution of several trees belonging to the climax stage of the Deciduous forest center: - - - - -, *Acer saccharum*; — — — — —, *Fraxinus americana*; — — — — —, *Fagus americana*; — — — — —, *Quercus alba*; — — — — —, *Magnolia acuminata*; — — — — —, *Liriodendron tulipifera*.

the forest. This may be explained, not by the statement that the maple is a northern tree, but by the fact that its shade-enduring and shade-producing properties find no worthy competitor among the trees of the Northeastern Conifer formation, while at the south it is one of many species having the same characteristics.

In the mountain region of the southern Appalachians there is

an extension of the Northeastern Conifer forest. Probably it should be regarded as a subcenter, because of the large number of endemic forms present, and because many other species there attain their greatest development. There, it has been shown (Cowles, :01b) that the pine stage is followed by an oak society, which in turn gives way to the climax deciduous forest. This seems to correspond with the succession in certain parts of the

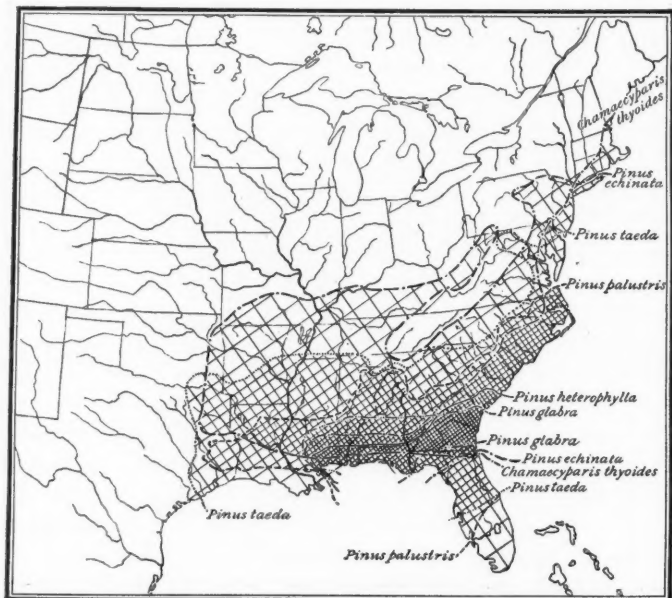


FIG. 4.— Map showing distribution of several trees belonging to the Southeastern Conifer forest center. *Chamaecyparis thyoides* is a common tree in the coastal swamps; the pines, with the exception of *Pinus glabra*, belong to the climax forest.

lower peninsula of Michigan, where the pines and the oaks both occur. Both localities are intermediate between the same two forest centers, and such a correlation is to be expected. The earlier stages in the succession are dominated by the Northeastern Conifers, while the last two are parts of the Deciduous forest center.

Furthermore in such intermediate regions, we may find two

distinct societies occupying the same or similar habitats. For example, in southern Michigan, the xerophilous bog societies and the hydrophilous swamp societies are so related. The former, however, are a part of the Northeastern Conifer forest, while the latter belong to the Deciduous forest succession. Consequently, where the bog societies are surrounded by oaks they

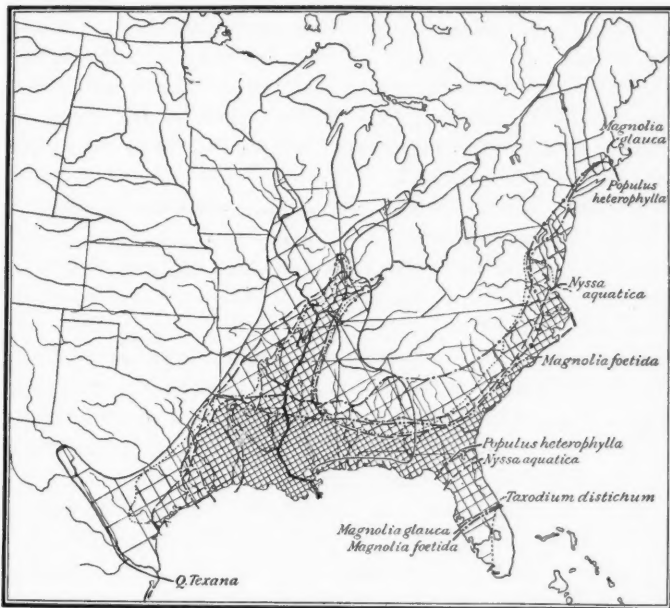


FIG. 5.— Map showing the distribution of some of the swamp trees of the Southeastern Conifer forest center. *Magnolia glauca*, *M. foetida*, *Nyssa aquatica*, *Populus heterophylla*, *Taxodium distichum*, and *Quercus texana*.

bear no successional relationship, while the swamp societies change gradually into the oak and climax stages of the Deciduous forest. In such cases the geographic considerations are of equal importance with the physiographic, for the proper classification of the plant societies.

Turning to the coastal plain of the southeastern states, we find a dominant forest of Conifers, with mixed Conifer and broad-leaved societies on the low grounds. Here slight differ-

ences of elevation and relative geological age tend to be strongly expressed in the vegetation (Pinchot and Ashe, '97, pp. 143-181; Mohr, :01, pp. 107-133; Harshberger, :04, pp. 611-614). The Conifers probably represent the climax forest of this formation. The distribution of certain of its components is shown in Figs. 4 and 5. Several other associations of shrubs and trees might be similarly depicted and still further emphasize the identity of the Southeastern Conifer forest center. As shown by the accompanying maps and the descriptions of Smith, and Pinchot and Ashe, there is a mingling of societies of this center and of the Deciduous forest, in the region of the Piedmont plateau, which tends to obscure the recognition of the stages properly belonging to each.

On the southern half of the Florida peninsula is a fourth formation, made up largely of xerophilous tropical species. It really represents the northern border of a center which dominates the West Indies and tropical America. It may be designated the Insular Tropical forest center.

There appear then to be four centers of distribution in eastern North America: (1) the Northeastern Conifer, (2) the Deciduous, (3) the Southeastern Conifer, and (4) the Insular Tropical. Each is made up of many societies, which bear a definite successional relationship to one another.

With the exception of the tropical, each of these formations has its western border marked by gradation into the grasslands of the Great Plains. The local flora of any part of the intermediate prairie region is composed of societies from the plains and the adjoining forest centers. For example, take the succession of plant societies on the bluffs of the Kansas River in eastern Kansas. The pioneer society is made up of *Bouteloua hirsuta*, *Mentzelia oligosperma*, *Euphorbia marginata*, *E. dentata*, *E. petaloidea*, *Bæbera papposa*, *Artemisia ludoviciana*, *Aster sericeus*, *A. fendleri*, *Megapterium missouriense*, *Tragia ramosa*, *Baptisia bracteata*, *B. australis*, *Lacinaria punctata*, *Croton texensis*, *Solidago missouriensis*, and *Silphium laciniatum*. This society belongs to the flora of the Great Plains and has its eastern limit in the prairie belt. The shrub stage following this is made up principally of *Symphoricarpos symphoricarpos*, *Ceanothus ovatus*,

Rhus glabra, *R. aromatica*, *R. radicans*, *Cornus asperifolia*, *C. amomum*, and *Xanthoxylum americanum*. This society is of very different origin and represents the western border of the shrub stage of the Deciduous forest formation. The shrubs are succeeded by trees belonging to the same center, among which are *Juniperus virginiana*, *Ostrya virginica*, *Celtis occidentalis*, *Quercus acuminata*, *Cercis canadensis*, *Ulmus fulva*, etc. A very different combination of societies would be met with in similar situations in northwestern Minnesota or southeastern Texas because of the different centers involved.

The mapping of these centers naturally brings up the question of the climatic determinants of each. During glacial times the Northeastern Conifer must have been mixed with the Deciduous forest. Why are they so distinctly separated at the present time? What are the causes of the "prairie peninsula" in Iowa, Illinois, and Indiana; and the region of open forests adjoining it? Naturally we look for some method of mapping climatic data, which will show climatic centers in approximately the same positions as the centers of plant distribution. An examination of monthly, seasonal, and annual temperature and rainfall maps shows that neither of these factors alone can do this. Historical considerations may aid in explaining the relative positions of these centers, but are inadequate for the complete explanation of their present limits.

A method was accordingly sought by which temperature and moisture data could be combined in a single number. The fact that so large a part of all plant adaptations is directly or indirectly connected with transpiration, suggested that if the ratio of the rainfall to the evaporation were determined, a new basis for mapping would be at hand which would involve several climatic factors. The depth of evaporation depends upon (T. Russell, '88) the temperature of the evaporating surface, the relative humidity of the air, and the velocity of the wind. These are the same climatic factors which most powerfully affect transpiration, and which must be of great importance in determining the geographic range of plants. Unfortunately, the only figures for evaporation available are those published by T. Russell for the year beginning July 1, 1887, and extending to July 1, 1888. They

represent the possibilities of evaporation from a free water surface inside the instrument shelters. Just as the figures for the rainfall do not represent the amount of water actually available for plants (since it includes the run-off, the part that evaporates, and that which sinks into the ground) so the figures for evaporation do not correspond to the water vapor actually given off by plants, because this is determined largely by the ecological adaptations of the individual plants. But the figures have a comparative value in both cases and when combined probably give a fairly correct idea of the distribution of these climatic factors in the eastern United States. The map was not extended to the western states owing to the paucity of data and the disturbing influence of the mountains. However, sufficient evidence is at hand to show that a desert center is clearly indicated in southern Arizona and California, and a forest center in the Puget Sound region. A comparison of the data for Colorado Springs and Pike's Peak indicates that the ratio increases from about 20 percent to 100 percent as one goes from the base to the summit of the Peak. This suggests the importance of taking other factors than temperature into account when explaining the distribution of the forests on mountains.

Turning now to the map (Fig. 6) showing the distribution of the rainfall-evaporation ratios in the eastern states, it will be noted that the Great Plains are marked by a rainfall equal to from 20 to 60 percent of the evaporation called for. The prairie region where forests are confined to the low grounds, is indicated by a ratio of from 60 to 80 percent. Its limits as indicated show a remarkable agreement with the actual distribution of the prairie. The region indicated by ratios between 80 and 100 percent is more or less coincident with the occurrence of "oak openings," "open forests," and "groves" on the uplands, and dense forests on the low grounds.

The southeastern area where the rainfall is from 100 to 110 percent of the evaporation, corresponds to the region of the Deciduous forest center. The distribution of the ratios above 110 percent in the region of the coastal plain is remarkably similar to the position of the Southeastern Conifer forest center.

In the southern Appalachians the ratio also rises above 110 percent and coincides with the occurrence of the southern extension of the northeastern forests. No data are available for the mountainous parts of Pennsylvania, so that this apparently isolated area may be climatically connected northward along the

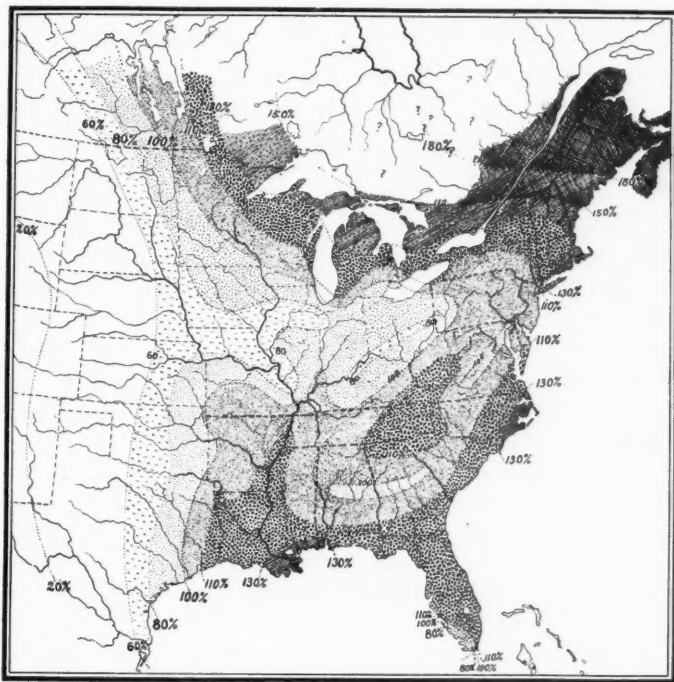


FIG. 6.—Map showing ratio of rainfall to evaporation expressed in percentages. (Compare with Sargent's map of the "Forests of North America," 10th Census Report.)

higher mountain crests. The Northeastern Conifer forest center is marked by ratios above 100 percent and centering in the St. Lawrence basin. It is probable that the northern limits of this formation will not be indicated by the rainfall-evaporation ratios, for the factors commonly accepted (Schimper, :03, p. 168) as determining the northern limits of forests are very different from those causing the boundaries of other formations. It should

also be stated that since climates are constantly changing and effects may lag far behind their causes, no map of present climatic conditions can hope to do more than approximate the present distribution of plants. Geographic and historical relations must be constantly borne in mind.

SUMMARY.

It may be stated, by way of summary, that eastern North America is occupied by four great forest centers: (1) the North-eastern Conifer forest, centering in the St. Lawrence basin, (2) the Deciduous forest, centering in the lower Ohio basin and Piedmont plateau, (3) the Southeastern Conifer forest, centering in the south Atlantic and Gulf coastal plain, and (4) the Insular Tropical forest of the southern part of the Florida peninsula, centering in the West Indies. The term center as here used, implies the idea of distribution about a region where the plants attain their best development. Such vegetation divisions are not fixed, but move and increase or decrease in extent depending upon continental evolution and climatic change.

Each formation is made up of many societies, bearing a definite successional relationship to one another, which being dependent upon soil factors may be best correlated with physiographic changes. In regions intermediate between centers, the local order of succession is made up of societies from each of the adjoining formations.

It has been found that if the ratios produced by dividing the amount of rainfall by the depth of evaporation for the same station, be plotted on a map they exhibit climatic centers which correspond in general with the centers of plant distribution. Further, the distribution of grassland, prairie, open forest, and dense forest regions is clearly indicated.

This is explained by the fact that such ratios involve four climatic factors which are of the greatest importance to plant life, *viz.*, temperature, relative humidity, wind velocity, and rainfall.

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MANDIBULAR AND PHARYNGEAL MUSCLES OF ACANTHIAS AND RAIA.¹

GUY ELLWOOD MARION.

INTRODUCTION.

THE following paper deals only with the muscles of the jaw and branchial region in the common dogfish (*Acanthias vulgaris*), and in one of the common skates (*Raia erinacea*). The existing literature upon this subject is very scanty, and aside from a few scattered references to the muscles, I have found only the detailed papers by Vetter ('74) upon the mandibular and branchial regions of the sharks, and a similar paper by Tiesing ('95) who discusses in the same way the muscles of the skates. Drüner (:03) uses the Selachians in describing the visceral muscles of the Urodeles.

The present article follows very closely the work of Vetter and Tiesing, especially that of the former. Tiesing classifies and arranges the muscles upon the basis of innervation; Vetter upon that of position and function. That the former method has its advantages is admitted, but convenience leads me to adopt the scheme of Vetter; and although not agreeing with him in all points, I have adopted as far as possible his nomenclature and lettering of the figures. As was said above, Vetter deals only with the sharks, and Tiesing with the skates, while I have tried to draw homologies between the two groups, and this has led me at times to differ from my predecessors.

The mandibular and branchial muscles may be divided into four main groups:—

1. Superficial circular muscles.
2. Interarcuales (muscles between the upper ends of the branchial arches).
3. Adductores (flexors at the middle of the arches).

¹ Contributions from the Biological Laboratories of Tufts College, No. XLIII.

4. Ventral longitudinal muscles.

Each of these in turn contains several muscles which are capable of arrangement under subordinate headings. In the following account, the muscles of one of the major divisions will be described for *Acanthias*, and then the corresponding muscles for *Raia*.

SUPERFICIAL CIRCULAR MUSCLES.

Of these there are seven groups:—

1. Superficial constrictors; *a*, dorsal; *b*, ventral.
2. Interbranchiales (lying between the walls of the gill clefts).
3. Levator maxillæ superioris (raising the upper jaw).
4. Trapezius (raising the shoulder girdle and drawing it forward).
5. Levator labialis superioris (raises the upper lip).
6. Levator rostri (raises the rostrum). In *Raia* only.
7. Depressor rostri (depresses the rostrum). In *Raia* only.

Superficial Constrictors.

Acanthias.

The superficial constrictors are the most external of the muscles which cover the gill pouches and form the surface of the region of the 'neck.' They may be divided, from position, into dorsal and ventral constrictors and are six in number on either side. Between them the five gill slits are placed, the first lying between the second and third, the fifth gill slit occurring behind the sixth constrictor (Figs. 1, 2). The gill slits are slit-like in character, about 18 mm. in extent, and are vertical in position, located near the ventral portion of the side of the body.

Dorsal Constrictors.—The first and most anterior dorsal constrictor (Fig. 2, *Csd 1*) takes its origin from the lateral surface of the cranium just below the posterior end of the dorso-lateral ridge. Its point of origin is not separated from that of the levator maxillæ superioris, to be described below. Its fibers run ventrally and forward, curving around the anterior wall of the

spiracle in front of the spiracular cartilages, and are inserted upon the inner surface of the lower jaw just below the 'coro-

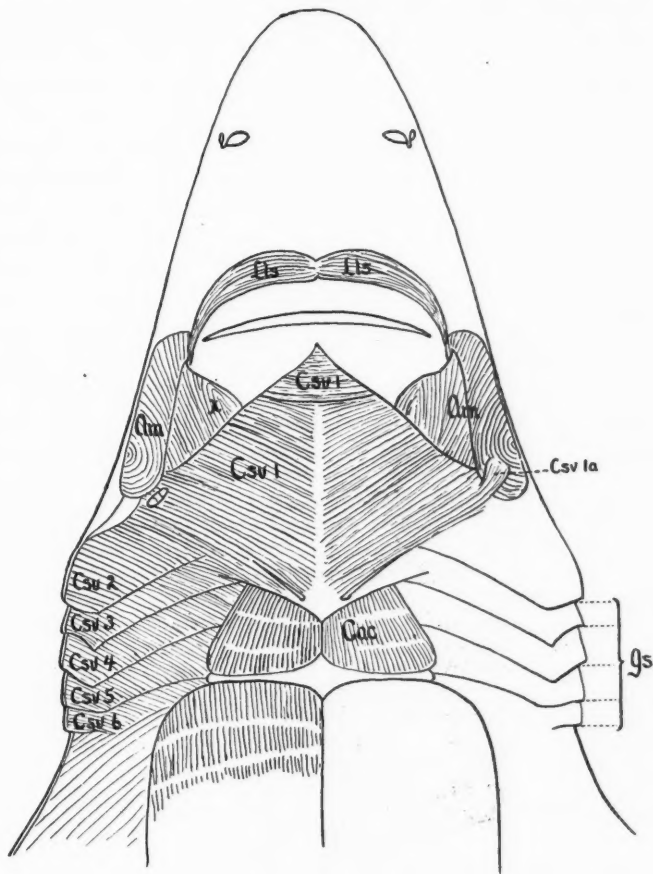


FIG. 1.—Ventral muscles of *Acanthias* after removal of skin. *Am*, adductor mandibularis; *Cac*, coraco-arcualis communis; *Csw 1-6*, constrictores superiores ventrales; *Csw 1a*, constrictor superioris ventralis, anterior fibers; *Gs*, gill slits; *Lls*, levator labialis superioris; *x*, tendon in adductor mandibularis.

noid' process. The general course of the fibers is curved, while that of the levator maxillæ superioris is straight, the only

feature distinguishing these two muscles, which Vetter does not regard as separate. I believe that of this common mass of muscles the anterior straight fibers alone represent the true levator maxillæ superioris, while the posterior curved fibers represent a

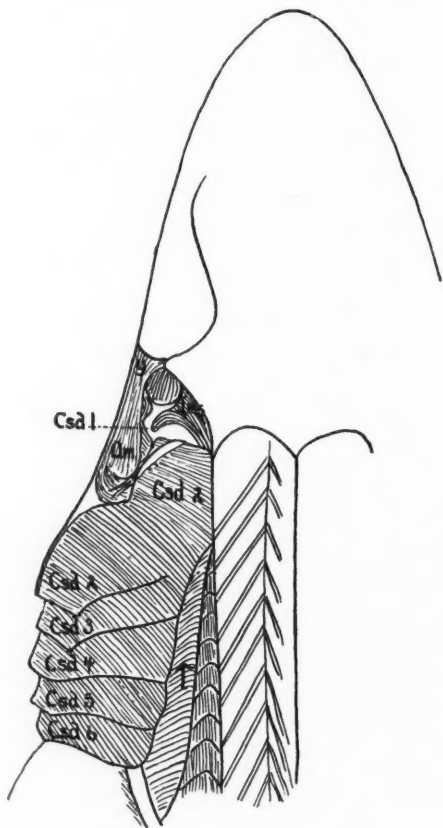


FIG. 2.—Dorsal muscles of *Acanthias* after removal of the skin. *Am*, adductor mandibularis; *Csd 1-6*, constrictores superiores dorsales; *Lms*, levator maxillæ superioris; *y*, tendinous mass back of eye; *T*, trapezius.

dorsal constrictor. In this connection Vetter ('74, pp. 420-421) says: "Die beiden Spritzlochknorpeln, welche fast senkrecht

zum Faserverlauf dieser Partie nach aussen gerichtet sind, lagern sich dabei ihrer hintern Fläche dicht an, so dass diese zu den Spritzlochknorpeln genau in dieselber Beziehung tritt, wie sie zwischen den *Mm. interbranch.* und den knorpeligen Radien des Kiemenbogen, oder zwischen *Csd 2* und *Csv 2* und den Radien des Zungenbeinbogen besteht."

Vetter has not carried his comparisons far enough. If these fibers nearest the spiracular cartilages bear the same relation to these cartilages as do those of the second dorsal and ventral constrictors to the rays of the hyoid arch, then why do they not represent another constrictor muscle *Csd 1* exactly like *Csd 2* in general relations? By a further comparison with *Raia* (Fig. 6) we see that the general course of the fibers of the posterior part as well as the insertion make this part distinctly comparable to the *Csd 1* of that form.

The second dorsal constrictor (Fig. 2, *Csd 2*) is by far the largest of the dorsal constrictors. It is a wide flat muscle extending from just behind the spiracle to the first gill slit. In front it arises from the postero-lateral surface of the cranium, farther back from the strongly fibrous fascia which completely covers the dorsal muscles. This origin extends as far back as the anterior end of the trapezius (Fig. 11) and even beyond that the fibers send tendinous attachments through the trapezius to their origin in the main tendinous fascia covering the longitudinal muscles. The first dorsal aponeurosis between the constrictors runs from the point where the fibers enter the trapezius in an obliquely ventral direction to the dorsal end of the first gill cleft. From this aponeurosis the more posterior fibers of *Csd 2* take their origin. The fibers of the muscles run obliquely from their origin on the dorsal margin of the muscle.

The insertion is also diverse. The most anterior fibers, which bound the spiracle behind, are inserted at the quadrate end of the upper jaw. The next fibers run around and cover the hyomandibula and are inserted upon the ceratohyal cartilage. This portion of the muscle corresponds to the levator hyomandibularis of *Raia*, where, attached to the same visceral arch, it has become much further developed. Beyond this portion the fibers are inserted upon a tendinous bridge connecting the dorsal and ven-

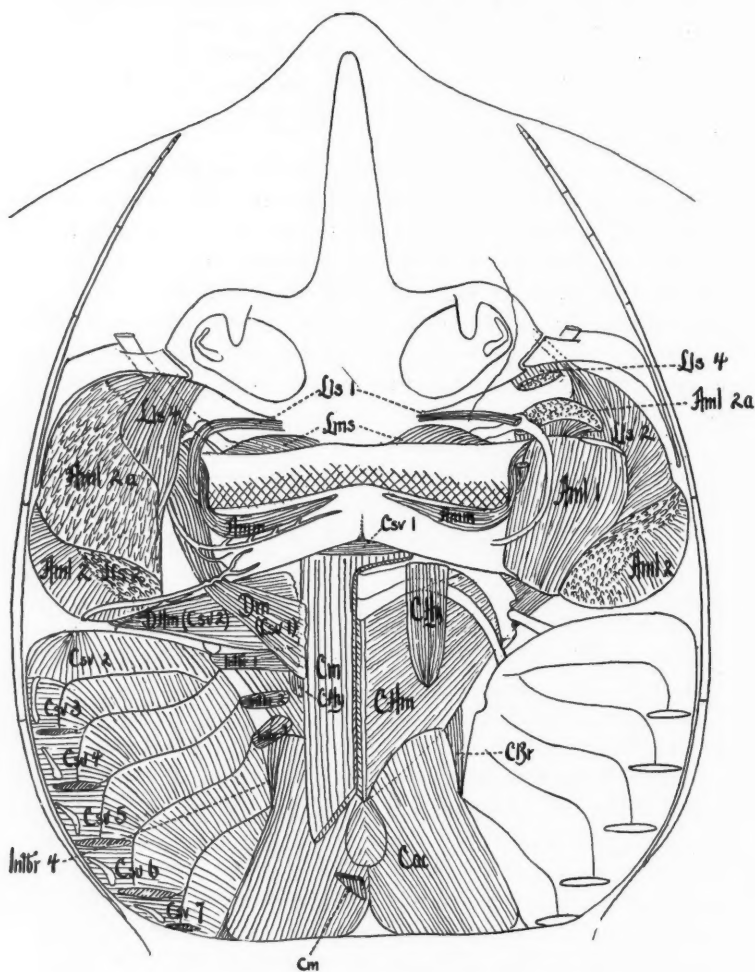


FIG. 3.—Ventral view of *Raia*, the right half a deeper dissection than the left. *Aml 1, 2*, adductores mandibularis lateralis (superficial layer, posterior); *Aml 2a*, adductor mandibularis lateralis (superficial layer anterior); *Amm*, adductor mandibularis medialis; *Cac*, coraco-arcualis communis; *CBr*, coraco-branchialis; *CHm*, coraco-hyomandibularis; *CHy*, coraco-hyoideus; *Cm*, coraco-mandibularis; *Csw 1-7*, constrictores superiores ventrales; *DHm*, depressor hyomandibularis; *Dm*, depressor mandibularis; *Intbr 1-4*, interbranchiales; *Lls 1-4*, levatores labialis superioris; *Lms*, levator maxillae superioris.

tral constrictors. This bridge extends about halfway from the end of the hyoid arch to the first gill slit. The remaining fibers pass over into those of the ventral constrictors, forming a continuous muscle. The fibers follow the direction of the gill slit in their course.

The remaining dorsal constrictors (three to six) are so closely similar that one description will serve for all (Fig. 2). The tendinous aponeuroses between them are somewhat curved, each ending at the top of a gill cleft and covering an underlying extrabranchial cartilage. The muscle fibers run nearly vertically and those attached to the aponeuroses are often also attached to the extrabranchials. Towards the dorsal margin some of the fibers converge to a tendon at the posterior edge of the muscle, and these tendons, after piercing the trapezius (Fig. 11, *Csd* 2-6), have their points of origin among the fibers of the dorsal longitudinal muscles, the last being also attached to the shoulder girdle. The more ventral fibers arise from the aponeurosis behind each muscle and are in part inserted on the aponeurosis in front, and in part continuous with the fibers of the ventral constrictors.

Ventral Constrictors. — The ventral constrictors (*Csv*) do not differ markedly from the dorsals, and like them are six in number. Here I am at variance with Vetter ('74, p. 416) who does not describe a first ventral constrictor for *Acanthias*, but begins with *Csv* 2. This is, however, clearly the first ventral constrictor, while his *Csv* β 2 is really the *Csv* 2, for if we compare ventral with dorsal sides, we find that the muscle in front of the spiracle which is inserted on the upper jaw is, as *Raia* shows, the first, while that upon the hyoid is the second dorsal constrictor. Just so, upon the ventral side the muscle attached to the lower jaw should be designated *Csv* 1, that upon the hyoid, *Csv* 2. With this exception my account of the ventral constrictors agrees well with that of Vetter.

On removing the skin and dissecting away the large amount of connective tissue upon the ventral side of the body (Fig. 1), we find immediately in front of the pectoral girdle, a pair of muscles, the coraco-arcuales communes (*Cac*) which, running forward, soon disappear under large sheets of muscle (*Csv* 1, 2).

which have their origin from a median line of aponeurosis and run obliquely forward and laterally to the cartilage of the lower jaw. This median aponeurosis starts at the level of the first gill slit, about half an inch in front of the pectoral girdle, and

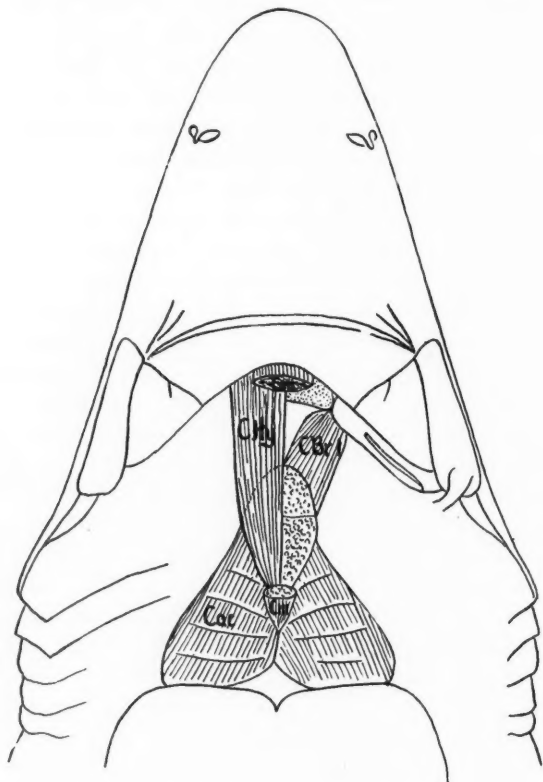


FIG. 4.—Ventral view of *Acanthias* showing the ventral longitudinal muscles. The right half a deeper dissection than the left. *Cac*, coraco-arcualis communis; *CBr 1*, coraco-branchialis; *CHy*, coraco-hyoideus; *Cm*, coraco-mandibularis.

extends to within half an inch of the symphysis of the lower jaw. The other ventral constrictors (*Csv 2-6*) are visible at either side of the coraco-arcuales communes.

The first ventral constrictor (Fig. 5, *Csv 1*) arises from the

median aponeurosis in common with, but ventral to, the second (*Csv 2*). Its fibers run obliquely forward and are inserted by means of small tendinous portions upon the ventral edge of the lower jaw. A few of the more posterior fibers (*Csv 1a*) are

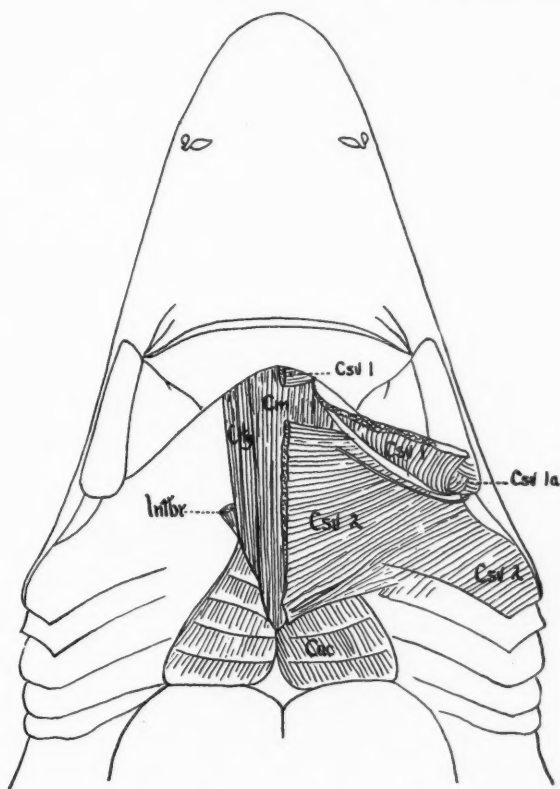


FIG. 5.—A deeper dissection of *Acanthias*. On the right, *Csv 1* has been turned back to show the whole of *Csv 2*. *Cac*, coraco-arcualis communis; *CHy*, coraco-hyoideus; *Cm*, coraco-mandibularis; *Csv 1-2*, constrictores superiores ventrales; *Csv 1a*, constrictor superioris ventralis, anterior fibers; *Intbr*, interbranchiales.

inserted upon the adductor of the lower jaw instead of upon the Meckelian cartilage, and here the fibers of *Csv 1* and *Csv 2* become fused so that at this point there is no sharply defined

margin to the first constrictor. In front the fibers of this muscle are not separated by a median aponeurosis, but run from one half of the jaw to the other.

Like the second dorsal, the second ventral constrictor (Fig. 5, *Csv 2*) is much the largest of the series. It does not extend as far forward as *Csv 1*, but, on the other hand, it extends back to the first gill cleft. About half of its fibers arise from the median aponeurosis, run parallel with those of the first ventral constrictor, and are inserted on the ventral edge of the ceratohyal cartilage. The posterior fibers, on the other hand, have their origin in the aponeurosis separating the second and third ventral constrictors, and, as they become too posterior to find attachment to the lower jaw or to the ceratohyal, they are inserted upon the fibrous bridge mentioned in connection with the second dorsal constrictor (p. 895), while still farther back the fibers run over into those of the first dorsal constrictor, passing in front of the first gill slit and running parallel to its margin.

The remaining ventral constrictors (*Csv 3-Csv 6*) are closely similar to each other, the only difference being in the points of origin. Excepting 3 and 6, the origin is either in the aponeurosis between each and the next succeeding muscle, or, in the case of the median fibers, from the fascia between the gill cavities and the common coracoid muscles. The most medial fibers of the second muscle take their origin, like those of *Csv 2*, in the median line ventral to the common coracoids, while the sixth has its origin in the pectoral girdle and in the fascia covering the ventral fin-muscles. The fibers of all of these muscles are either inserted in the aponeurosis in front, or are continued dorsally and laterally over into the dorsal constrictors.

The function of the constrictors is to compress the pharyngeal chamber, eject the water, and close the gill slits. The first dorsal constrictor may assist in raising the upper jaw, and the second may raise the hyoid arch, while the first and second ventral constrictors lower the under jaw and the hyoid respectively, thus assisting in the opening of the mouth.

Raia.

In removing the skin from the skate, there is less connective tissue than in *Acanthias*, the constrictors are not so conspicuous, and more muscles occur, as for instance those which control the rostrum. The muscles, too, have been altered in relative size and position in accordance with the modification of form in this extreme type, but the same general relations are easily followed.

The constrictors have increased in number to seven, and, associated with the extreme flattening of the branchial region, the dorsal and ventral constrictors are not continuous as in *Acanthias*, but are distinct, being separated at the lateral part of the branchial region by what Tiesing has called the horizontal tendon. This tendon starts from the lateral end of the hyomandibular cartilage, and running along the anterior surface of the gill region, connects with the propterygium and continues back in the lateral branchial region, affording insertion to both dorsal and ventral constrictors. Since the gill slits lie wholly upon the ventral surface, the ventral constrictors in turn have divided into median and lateral portions, the line of division occurring at the median ends of the gill clefts (Fig. 6).

Dorsal Constrictors.—The first dorsal constrictor (Fig. 6, *Csd 1*) takes its origin from the lateral labyrinth region of the skull, ventral and posterior to the postorbital process, and is continuous posteriorly with the levator maxillæ superioris, these two muscles, as in *Acanthias*, having a common origin. The fibers run forward, curving laterally along the anterior margin of the spiracle, and are inserted on the dorsal surface of the hyomandibula, a short distance from its anterior end. A sheet of fascia (*F*) to be described later, has a part of its origin from this muscle near its insertion; in part it also arises from the posterior margin of the spiracle.

The second dorsal constrictor (*Csd 2*) is larger and more differentiated than in *Acanthias*, having developed into distinct muscles with different functions—an anterior levator hyomandibularis and a posterior portion which agrees with the other constrictors in position and shape.

The levator hyomandibularis (*LHm*) arises from the postero-

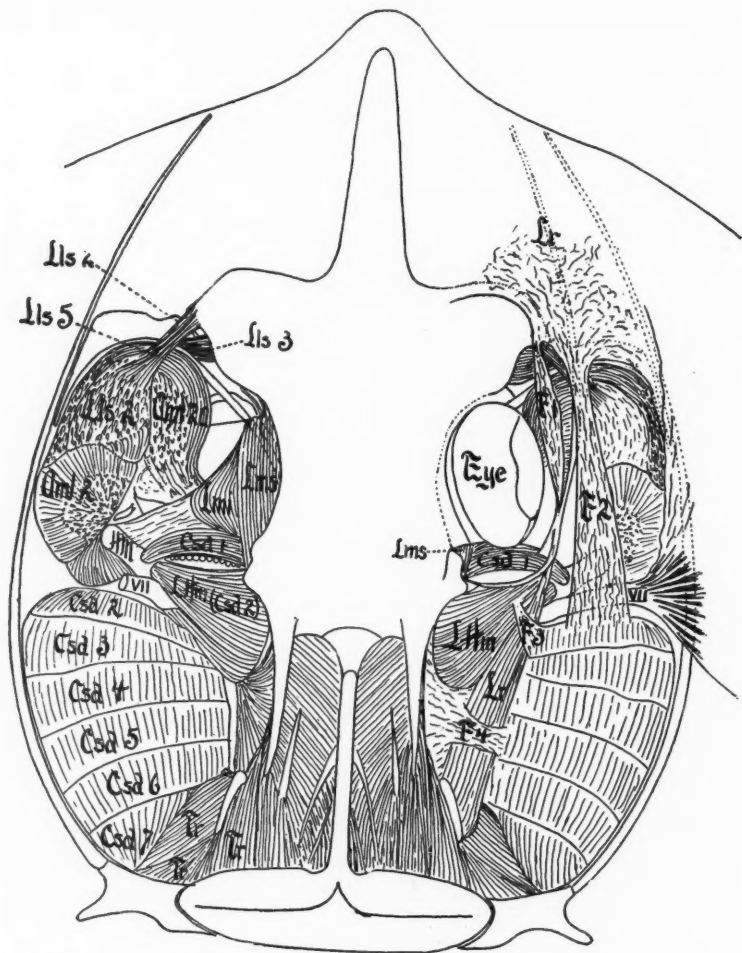


FIG. 6.—Dorsal view of *Raia*, more deeply dissected on the left. *Aml 2*, adductor mandibularis lateralis (superficial layer, posterior); *Aml 2a*, same, superficial layer, anterior; *Csd 1-7*, constrictores superiores dorsales; *F 1-4*, fasciae; *HM*, hyomandibula; *LHM*, levator hyomandibularis; *Lls 2, 3, 5*, levatores labialis superioris; *Lmi*, levator maxillae inferioris; *Lms*, levator maxillae superioris; *Lr*, levator rostri; *Tr*, trapezius.

lateral part of the labyrinth region of the cranium. Its fibers run obliquely forward and outward, forming the posterior wall of the spiracle, while the large lateralis nerve penetrates the middle of the muscle in order to reach the region of the fin. The muscle is inserted upon the hyomandibula, the line of insertion beginning behind that of the first dorsal constrictor and extending the length of the rest of the cartilage. This muscle has become differentiated from the rest of the constrictor system and is only used to raise the hyomandibula.

The other more lateral and posterior portion of the second dorsal constrictor (*Csd 2*) is associated with the others of the series. Its fibers are entirely distinct from those of the levator hyomandibularis and arise from the tendon separating the second and third constrictors. This tendon is not so extensive as the succeeding and does not extend laterally to the horizontal tendon which is correspondingly interrupted opposite this point.

The remaining dorsal constrictors (*Csd 3-7*) are practically alike. Each arises from the tendon between itself and the next following muscle and is inserted on the tendon in front. The seventh forms an exception in that it is smaller than the others, and its fibers are not parallel to the main axis of the body, but converge to the point of origin upon the shoulder girdle. The intermuscular tendons incline more and more from the transverse direction as we go farther back, and, as the muscles extend to the horizontal tendon, they bend downward at the lateral margin in order to reach it. A few of the fibers of (*Csd 3*) are inserted in a strong tendon (*F 3*) which extends forward from the intermuscular tendon between constrictors 2 and 3, ventral to all the adductors of the jaws, to be inserted on the skull and surrounding tissue lateral to the nostrils.

The ventral constrictors (Fig. 3, *Csv*) are likewise seven in number. The first, instead of forming a broad sheet as in *Acanthias*, is divided into two portions, an anterior part, which extends from one mandibular half to the other just behind the symphysis, and a posterior portion. The anterior portion is not constantly present; I failed to find it in one specimen.

The posterior part of the first ventral constrictor is a flat fan-shaped muscle which arises in connection with the depressor

rostri (to be described later) in the fascia covering the coraco-arcualis communis, and is inserted upon the mandible at about the center of its posterior edge. This part of this ventral constrictor thus forms a distinct depressor mandibuli (*Dm*). Only the anterior edge of the origin of this muscle can be seen until the depressor rostri (Fig. 15, *Dr*) is removed, but the method of description necessitates its mention here.

The second ventral constrictor is likewise much modified from the condition in *Acanthias*, being divided into an anterior depressor hyomandibularis (*DHm*) and a posterior second ventral constrictor proper (*Csv* 2).

The depressor hyomandibularis has its origin in the fascia overlying (ventral to) the coraco-hyoideus, the fascia connecting the depressors of the two sides dorsal to the coraco-mandibularis. The general course of the muscle is transverse to the longitudinal axis of the body. The fibers converge from a broad flat origin to a cylindrical muscle which then runs dorsally and becomes inserted upon the posterior end of the ventral edge of the hyomandibula and upon the horizontal tendon. The posterior portion of the second ventral constrictor has its origin in part in the tendon (less developed than the others) separating it from the third ventral constrictor, while the more lateral fibers are continuous with those of the third constrictor, there being no aponeurosis between them. The fibers run forward, converging from either side toward their insertion on the horizontal tendon.

Each of the remaining ventral constrictors (*Csv* 3-*Csv* 7) is composed of two parts, a large median and a smaller lateral portion, the muscle becoming smaller toward the lower limits of the gill region. The tendons separating the constrictors (the first two are united medially) run obliquely outward and backward to the median ends of the gill slits and then turn abruptly and pass to the middle of the gill slit behind, so that this portion of the tendon serves to separate the median from the lateral parts of the muscle.

The origin of the median portion of the seventh ventral constrictor is from the fascia covering the ventral edge of the coraco-branchialis. The other muscles arise from the tendon

behind. In all, the fibers are inserted upon the tendon in front, and their courses are somewhat oblique near the median side, and nearly at right angles to the body axis at their outer margins.

The lateral portions of the constrictors arise from the tendons between them and the median muscle, and the fibers run laterally to some small cartilages (not always present) and then turn dorsally to be inserted on the horizontal tendon.

Interbranchiales.

Acanthias.

It is a question whether these should be included among the superficial circular muscles or not, since they are in no sense

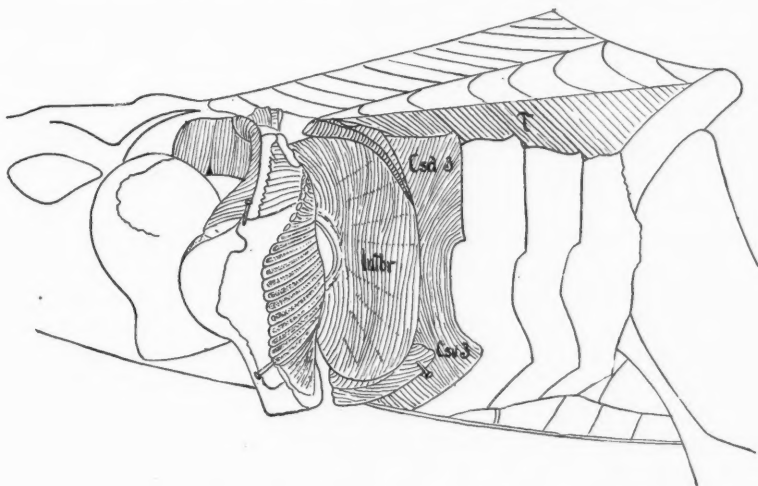


FIG. 7 — Lateral view of *Acanthias* to show the interbranchiales. *Csd 3*, constrictor superioris dorsalis 3; *Csw 3*, constrictor superioris ventralis 3; *Intbr*, interbranchialis; *T*, trapezius.

superficial, nor circular in the same sense that the other muscles are, and they lie in a different plane. However, they are closely allied with the constrictors in function, assisting in the general contraction and expansion of the gill basket, and since comparisons with Vetter are made easier, they are retained here.

These muscles (Figs. 5, 7, 8, 11, *Intbr*) are fewer in number and lie between the demibranchs of the four complete gills. Each is extremely thin and consists of a sheet of fibers, anterior to the cartilaginous gill rays, and extending between the gills

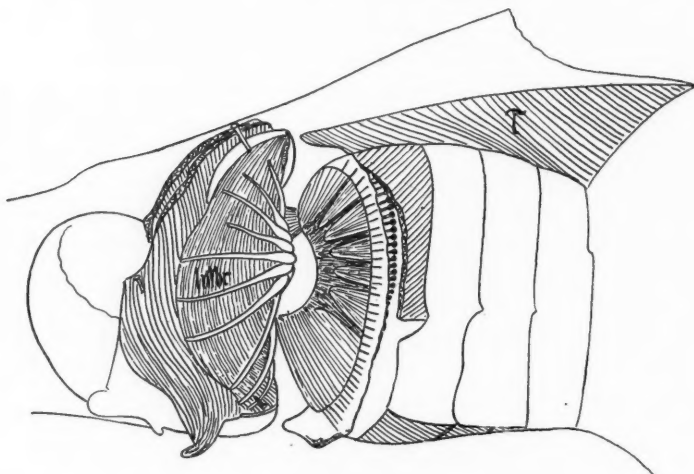


FIG. 8.—Lateral view of *Acanthias*, showing the interbranchiales (*Intbr*). *T*, *trapezius*.

from top to bottom of the septum. A tough white fascia extends from the dorsal longitudinal muscles to the extra-branchial cartilages, holding the latter in place below the aponeurosis between the dorsal constrictors, and connecting them with the interarcual muscles to be described later. The most dorsal of the interbranchial muscle fibers arise from the fascia just described, while the rest have their origin in the aponeurosis between the dorsal constrictors. The more median of the fibers curve outward and downward toward the median line, to become inserted on the anterior margin of the epibranchial cartilage (Fig. 7). The more lateral fibers are larger and follow a broad curve from the dorsal to the ventral side of the gill septum, and thus pass into the ventral fibers about to be described, just as the dorsal and ventral constrictors merge in part into each other.

The ventral fibers arise from the extrabranchials as well as

from the tendinous fasciæ connecting these cartilages, while the fibers on the median side arise from the fascia between the longitudinal muscles (Fig. 5 shows an instance of origin at the end of the common coraco-arcualis). This point is of some importance in the interpretation of the condition in *Raia*. The fibers near the middle line are inserted upon the anterior surface of the cerato-branchial cartilage, while the lateral fibers are continuous with those of the dorsal side as noted above. Often the muscle fibers stop at a gill ray, the tissue becoming aponeurotic, and then the muscle fibers continue on the other side.

These interbranchial muscles draw the gill radii together and thus aid in the contraction of the gill basket. In the case of the hyoid arch, the second dorsal and ventral constrictors replace the interbranchialis, since here the gill radii lie immediately beneath the surface (constrictor) muscles.

Raia.

The interbranchiales of *Raia* are much like those of *Acanthias* in position and number, the muscle of the first arch being replaced by the posterior part of *Csv2* and *Csd2*. Owing to the shape of the branchial region they do not form a continuous arc but are divided into a dorsal and a ventral portion, so that the line of division coincides with the angle separating the halves of each branchial arch. The muscle fibers of the dorsal portion arise from the aponeuroses between the dorsal constrictors, and run ventrally (Fig. 12) until they become inserted upon the dorsal surface of the epibranchial cartilages or upon the ray which runs out from the angle to the horizontal tendon. The ventral fibers take their origin from the tendons between the ventral constrictors and run dorsally to their insertion upon the ventral surfaces of the cerato-branchials or upon the horizontal ray just referred to. The fibers never become continuous, as in *Acanthias*, from dorsal to ventral surfaces. A few bundles of the most median fibers of the ventral portion are overdeveloped, and have extended so as to take their origin from fasciæ covering the coraco-mandibularis muscle (Fig. 3, *Intbr*). A similar condition was noted above for *Acanthias* but these fibers were not as

prominent there as here. Tiesing, basing his opinion on the work of Vetter upon *Heptanchus*, has regarded these fibers as a deeper layer of the constrictor but *Acanthias* shows this not to be tenable. There is no resemblance to a constrictor. In the case of the fourth arch the corresponding fibers extend into

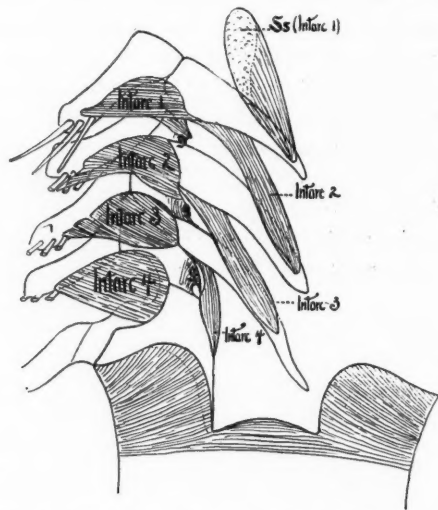


FIG. 9.—Dorsal view of gill arches of *Acanthias* to show the interarcuales. *g*, groove; *Intarc* 1-4, interarcuales; *Ss*, subspinalis.

tough tendons connected with the coraco-arcualis communis muscle (Fig. 3). On the dorsal side there is but one instance of this extension of the interbranchials (Fig. 6, at the inner posterior angle of *Csd6*). A few fibers take their origin from the sides of the first vertebra. This could not be considered a constrictor.

Levator Maxillæ Superioris.

Acanthias.

This muscle (Figs. 2, 11, 14, *Lms*), already mentioned in connection with the first dorsal constrictor, arises in common with it from the lateral surface of the cranium just posterior to the

postorbital process. It is larger than the first dorsal constrictor and fills the entire bay back of the postorbital process. The fibers extend anteriorly and ventrally to their insertion on the dorsal margin of the palatal process of the upper jaw, just anterior to the attachment of the first dorsal constrictor. In fact the only distinction that can be drawn is that in the levator the fibers go directly to the jaw while those of the first dorsal constrictor curve around the anterior margin of the spiracle.

Raia.

In the skate the levator of the upper jaw (Figs. 3, 6) is composed of a thick dorsal and a thinner ventral layer, the two united at their point of insertion. The thicker layer (*Lms*) arises from the side of the skull, just ventral to the postorbital process, and its fibers run almost straight forward, then dorsal and backward in front of the oral cavity to their insertion on the upper jaw. The thinner and more ventral layer (*Lmi*) arises just below and behind the facial foramen whence its fibers run forward, laterally, and backward to unite with the dorsal layer. This course involves a strong lateral bend from which a strip of fascia extends to the hyomandibular cartilage (Fig. 6). Some of the more ventral fibers are inserted in the membranous wall of the roof of the mouth.

Tiesing maintains that the levator maxillæ superioris is only a deeper part of the first dorsal constrictor,—a view rendered very probable from the relations in *Acanthias* in which the conditions are the more primitive. It is very similar to a constrictor in origin and function, although differing widely in form.

Trapezius.

Acanthias.

The trapezius (Figs. 2, 7, 8, 11, *Tr*) has its origin in fascia covering the sides of the dorsal longitudinal muscles. Its fibers arise from a straight line extending from the posterior end of the cranium to the dorsal part of the shoulder girdle, although the

muscle extends through only the posterior three fourths of this. The fibers, which become thinner posteriorly, run obliquely downward and backward, the majority being inserted on the anterior edge of the pectoral girdle, while the more anterior fibers turn directly downward and are inserted on the dorsal edge of the last branchial arch. At intervals tendinous strands of the dorsal

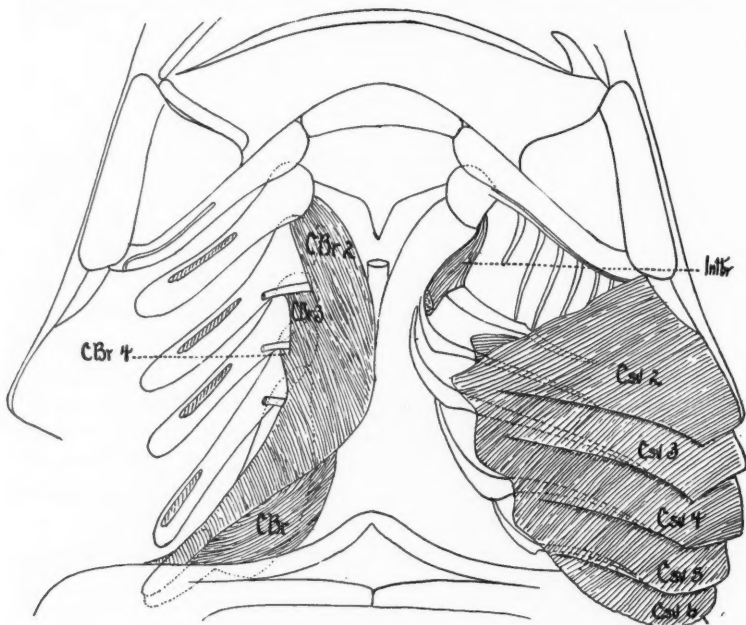


FIG. 10.—Ventral view of *Acanthias* showing the coraco-brachiales. *CBr*, coraco-brachiales; *Csd* 2-6, constrictores superiores dorsales; *Intbr*, interbranchialis.

constrictors (Fig. 11, *Csd*) as already described, pass through this muscle. The function of the trapezius is to raise the girdle and draw it forward.

Raia.

A trapezius has not been described in the skates but there occurs here a muscle (Fig. 6, *Tr*) which in its attachments and

the direction of its fibers somewhat resembles it although it does not in all respects fulfill the conditions found in *Acanthias*. There are here three parts to the muscle: a small median portion and two more lateral in position.

The median, the smallest, arises from the side of the first vertebra and its fibers run obliquely backwards to be inserted on the anterior edge and ventral surface of the suprascapula. The most lateral portion arises near the first and its fibers run obliquely backward and outward to the insertion upon the upper surface of the last visceral arch and on the anterior edge of the girdle far down towards the ventral edge. The remaining portion arises just ventral to the part just described and its fibers are attached to the scapular portion of the pectoral girdle. (In *Raia radiata* the median portion is greatly reduced and its origin is from the lateral process of the vertebra, just back of that of the next division.)

The two lateral portions of the muscle in *Raia* are apparently partly antagonistic, that first described elevating, the other depressing the girdle to a certain extent.

Levator Labialis Superioris.

Acanthias.

Although Vetter classifies this muscle among the adductors he says ('74, p. 448): "Er erscheint als seriales Homologon des *M. levator max. sup.* und aller der andern Theile des grossen Constrictors, welche vom Schadel oder von der epaxionischen Muskulatur zu der Visceralbogen gehen, und ist sonach passenden als *M. levator labii sup.* zu bezeichnen." For this reason I have included it among the other similar constrictors. This muscle (Fig. 1, *Lls*) has its origin from the ventral surface of the cranium, in front of the basal process and to one side of the middle line. The fibers run outwards and backwards, describing an arc to the angles of the mouth where they converge to a straight fibrous tendon which passes dorsal to the labial cartilages, crosses the angle of the mouth at right angles, and is inserted among the fibers of the adductor mandibularis.

Raia.

The levator labialis superior in the skate has been differentiated into five parts (Figs. 3, 6, *Lls 1-5*). Of these the first (*Lls 1*) most nearly resembles the single muscle of *Acanthias*. It is small, cylindrical, and arises from the ventral surface of the cranium near the orbit and just behind the base of the ethmoid process. It runs laterally and then backward to the angle of the mouth, which it passes, to become inserted in the fascia

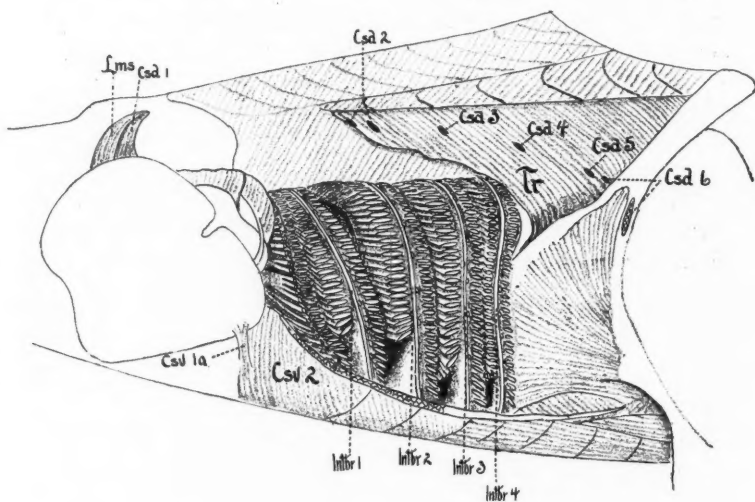


FIG. 11.—Lateral view of *Acanthias* showing interbranchiales and trapezius. *Csd 1-6*, constrictores superiores dorsales; *Csw 1a*, constrictor superioris ventralis, anterior fibers; *Csw 2*, constrictor superioris ventralis 2; *Intbr 1-4*, interbranchiales; *Lms*, levator maxillae superioris; *Tr*, trapezius.

between the adductores mandibularis medialis and lateralis which it separates.

The second division (Fig. 6, *Lls 2*) is much the largest of the labial muscles. It arises from the dorsal surface of the most lateral part of the ethmoid region in front of the antorbital process. The origin is small and of rather soft fibrous material. After passing dorsally of the large mass of the adductor man-

dibularis lateralis 2a, it widens into a large muscle which disappears under the adductor mandibularis lateralis 2 to become inserted on the mandibular cartilage while a portion of its fibers become confused with the posterior portion of *Aml* 2 (Fig. 3).

The third division (Fig. 6, *Lls* 3) is the smallest of the system: a short thick muscle running from the postero-lateral edge of the dorsal surface of the nasal capsule, laterally, to the posterior dorsal angle of the antorbital process, the fibers converging towards the insertion.

The fourth division (Fig. 3, *Lls* 4) is broad, thin, and flat, and its origin is continuous with and ventral to that of the third division. It lies upon the adductor mandibularis lateralis and covers a portion of it ventrally. The mandibularis branch of the fifth nerve runs between the two. Its general course is posterior and the fibers which are not inserted in the fascia covering the adductor mandibularis lateralis converge to a strong tendon, which makes its way through that muscle, to their insertion on the ventral surface of the mandible.

The fifth division (Fig. 6, *Lls* 5), though included by Tiesing among the muscles, is but a group of strong tendinous fibers having its origin just posterior to that of the second division and its insertion on the strong fascia enveloping that muscle. Muscular tissue is lacking in it, and it is scarcely more than a second origin of that muscle.

Levator Rostris.

This muscle (Fig. 6, *Lr*), together with the next, would be treated first among the superficial muscles were we describing *Rai* alone, but since it is lacking in *Acanthias* it has been left until now. Upon removing the skin from the dorsal surface, the levator rostris is the first seen and most superficial of the muscles. It takes its origin from the lateral edge of the lateral process of the first vertebra which projects above the surrounding muscles, and from the tendinous fascia covering the muscles in this region. The fibers run obliquely forward, converging to the region where they cross the levator maxillæ superioris and the first dorsal constrictor where they pass into a strong cylin-

drical tendon. This tendon continues forward, passing outside the spiracle and the eye and over the various jaw muscles and the antorbital cartilage, into the fascia of the rostral region where it is inserted in the strong membranous tissue stretching between the rostrum and the propterygium.

Depressor Rostris.

The depressor rostri (Fig. 15, *Dr*), the antagonist of the last, is a broad, flat, thin muscle arising from the fascia covering the coraco-mandibularis and from the fibers of the coraco-arcualis communis. The muscle extends forward and outward in the direction of the adductor muscles where some of the lateral fibers are inserted in the white fascia covering these muscles,¹ while the majority are collected into a strong tendon which extends forward, lateral to the nasal capsule and ventral to the antorbital process, then coming towards the median line is inserted in the membranous tissue between the tip of the rostral cartilage and the propterygium.

INTERARCUALES.

Acanthias.

The interarcuales (Fig. 9) are divided into two systems of muscles: one more medial, the other more lateral in position, each consisting of four muscles, similar in function, the first of the medial system being the subspinalis of Vetter ('74, p. 444).

Medial System.—The most anterior of the medial interarcuales has been treated as a distinct muscle, the subspinalis, by Vetter but as it agrees closely with the others in function and differs only in its origin from the rest, it is here regarded as but one of the set. Its origin is from the fascia on the under side of the dorsal longitudinal muscles, from the vertebræ near the cranium, and from the under side of the cranium itself just in front of the foramen magnum. From this broad origin it

¹ In *Raja radiata* most of the fibers have this insertion, while a small proportion are continued into the rostral depressor tendon.

tapers to a tendon which is inserted upon the dorsal posterior end of the first pharyngo-branchial. It draws the first pharyngo-branchial forward in the same way that the succeeding muscles draw the pharyngo-branchials upon which they are inserted.

The second, third, and fourth medial interarcuales arise from the posterior surface of the first, second, and third pharyngo-branchials respectively, a little in front of the middle of each and are inserted upon the dorsal surface of the second, third, and fourth pharyngo-branchials. The point of attachment is at about the middle of the cartilage except in the case of the second where the attachment is behind the middle. These muscles have a larger surface of insertion than of origin and decrease in size from in front backwards.

Lateral System.—A description of the first of the four will answer for the first three muscles of this system. The first lateral interarcuale has a double origin. The majority of the fibers arise from the posterior edge of the anterior end of the first pharyngo-branchial and a few from the anterior end of the second pharyngo-branchial just in front of the groove (*g*) for the passage of the blood vessel. The fibers are inserted on the dorsal surface of the epibranchial along a line which is a continuation of the line of insertion of the interbranchial muscle. Some of the fibers are inserted so far laterad as to be in front of the most dorsal gill rays, so that the muscle appears to be almost a portion of the interbranchial which has been forced deeper for its origin. The last lateral interarcuale differs from the rest only in its origin. Since the fourth and fifth pharyngo-branchials are fused the origin is not divided.

Raia.

The interarcuales are much reduced in the skate; indeed only the lateral system persists while the medial system is represented by non-muscular membranes connecting the pharyngo-branchial cartilages in the same way. Each of the muscles of the lateral system arises from the posterior edge of the anterior end of the pharyngo-branchial and is inserted upon the medial end of the epibranchial of the same arch.

It may be a question whether the interbranchiales, the interarcuales, and the adductores (next to be described) do not form a system of deep as opposed to the superficial constrictors. Each contributes toward the constriction of the whole branchial region, and, with the exception of the largest mandibular adductor, each lies beneath the more superficial system.

ADDUCTORES.

The adductor muscles draw together the ventral portions of each visceral arch. In the case of the mandibular arch they close the mouth, while in the gill arches they occur at the lateral hinge and approximate the ceratobranchial and epibranchial por-

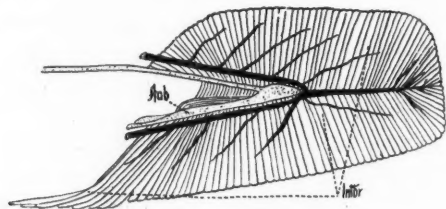


FIG. 12.—Anterior side of interbranchial muscle of *Raia*. *Aab*, adductor arcus branchialis; *Intbr*, interbranchiales.

tions of each. The adductors of the first (mandibular) arch are enormously developed in correlation with the use of these parts, while those of the gill arches are very small. In *Acanthias* the adductors are much simpler than in *Raia*.

Adductores Mandibulares.

Acanthias.

The mandibular adductor (Figs. 1, 2, 13, 14, *Am*) has a very strong tendinous envelope. Its fibers arise from the quadrate region of the upper jaw, and are attached to the entire lateral surface as well as to the medial surface of the muscle process on its dorsal margin. The course of the fibers is down-

ward and backward to the lower jaw where they are attached to the entire width of Meckel's cartilage. The details of the course of the fibers are rather difficult to express. On the lower jaw (Fig. 1) they extend nearer to the middle line than on the upper, and this portion (*x*) instead of coming from the fascia which separates it from the rest, comes from the posterior part of the upper jaw. A strong tendon is attached to this part which runs forward into the levator labialis superioris muscle. Other fibers are specialized in function. A broad thin sheet of fibers is extended on the upper half of the adductor and has its true origin from the under surface of the postorbital process, while a strong mass of tendinous material at the angle of the eye (Fig. 13, *y*) gives origin to some of the fibers. A few fibers of the first ventral constrictor, which have already been referred to as *Csv 1a*, are attached to the outer surface of the adductor.

Raia.

In the skate the adductor muscles are more complicated. They cover and surround the lateral ends of the jaws and are divided into distinct and easily separated layers. Following Tiesing, they may be grouped into a small medial, and a larger lateral portion, the latter in turn divisible into deeper and superficial layers.

Adductor Mandibularis Medialis.—This, the smallest of the adductors (Figs. 3, 6, *Amm*) arises from the anterior edge of the upper jaw. Its fibers run back across the angle of the mouth and then medially to become inserted near the anterior (occludent) margin of the lower jaw not far from the symphysis. Its origin is in common with the deeper layer of the lateral adductor and the two separate where the levator labialis superioris passes to become attached to the fascia between them.

The *adductor mandibularis lateralis* is subdivided into a deep layer (Figs. 3, 6, *Aml 1*), and a more superficial portion (*Aml 2* and *Aml 2a*). The deep layer is largely covered by the superficial. The majority of its fibers arise from the anterior edge of the upper jaw as well as from the entire outer surface of the muscle process, and they find their insertion upon the outer surface of the lower jaw about opposite the point of origin.

The second division of the levator labialis superior, in its course to its insertion on the ventral surface of the lower jaw, crowds into the superficial layer of the lateral mandibular adductor, separating it in part into anterior and posterior portions. The anterior of these divisions (*Aml 2a*) arises in part from the dorsal surface of the lower jaw, directly opposite to its point of attachment to the deeper layer, and in part from the ventral

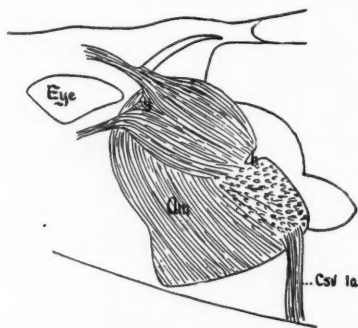


FIG. 13.—Lateral view of adductor mandibularis of *Acanthias*. *Am*, adductor mandibularis; *Cst 1a*, constrictor superioris ventralis, anterior fibers; *y*, tendinous mass back of eye.

surface by means of a very strong fibrous tendon. It runs forward, passing dorsally to the upper jaw and immediately broadens out into a large mass of fibers which curve ventrally and run backward, covering the deeper layer of the adductor and finally becomes inserted upon an aponeurosis surrounding the deeper layer. From this aponeurosis the fibers start again and continue backward, completely encasing the ends of both jaws, to the insertion directly and by means of tendons upon the lower jaw.

Adductores Arcus Branchialis.

The hyomandibular and hyoid cartilages are bound together at their articulation by strong ligaments, but no adductors are present connecting the two. In the branchial arches proper such muscles occur.

Acanthias.

A few short adductor muscle fibers extend between the cerato- and epibranchial cartilages of each branchial arch. They have their origin in small grooves on the inner surface of the epibranchials and are inserted in similar grooves on the inner (dorsal) surfaces of the ceratobranchials. Their function is to flatten the branchial region.

Raia.

In the skates (Fig. 12, *Aab*) the adductors of the branchial arches closely resemble those of *Acanthias*. They arise from

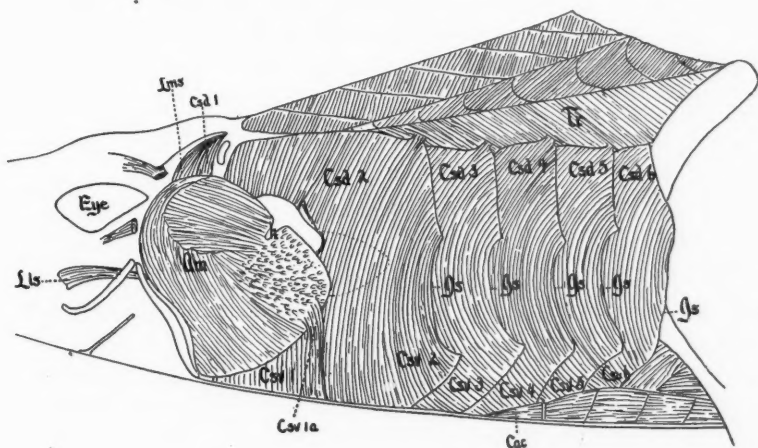


FIG. 14.—Side view of *Acanthias* after removal of the skin. *Am*, adductor mandibularis; *Cac*, coraco-arcualis communis; *Csd 1-6*, constrictores superiores dorsales; *Csv 1-6*, constrictores superiores ventrales; *Csv 1a*, constrictor superioris ventralis, anterior fibers; *Gs*, gill slits; *A*, hinge of jaws; *Lis*, levator labialis superioris; *Lms*, levator maxillae superioris; *Tr*, trapezius.

and are inserted in similar grooves in epi- and ceratobranchial cartilages, while a few of the fibers extend some distance along the ceratobranchial before finding their insertion.

VENTRAL LONGITUDINAL MUSCLES.

The location and character of these muscles is apparent from this name. In *Acanthias* they are usually thick and solid, while, correlated with the depressed body, they are flat and thin in *Raia*.

Coraco-mandibularis.

Acanthias.

In the dogfish the coraco-mandibularis is an azygos muscle lying in the median line of the body, and is exposed (Fig. 5, *Cm*) by removing the ventral constrictors. It is the most superficial of the ventral longitudinal muscles. It arises from the fascia between the coraco-arcuales communes and its fibers rapidly diverge near the origin, where the muscle is nearly circular in section, to form a flattened band which is inserted on the posterior edge of the lower jaw on either side of the symphysis.

Raia.

In the skate the coraco-mandibularis (Figs. 3, 15, *Cm*) also lies in the median line but is not covered by the ventral constrictors, since these are here more lateral in position, with the exception of a few fibers (Fig. 3, *Csv I*) already described. In origin and insertion there is a close agreement with *Acanthias*, but the muscle is thinner and flatter than in that form. With the exception of the depressor rostri and the depressor mandibuli, whose origins overlap its margin, it is the most superficial of all the ventral muscles.

Coraco-hyoideus.

Acanthias.

The coraco-hyoideus muscles (Fig. 4, *Chy*) are exposed by removing the coraco-mandibularis, which lies close to the median line. They are the largest of the ventral longitudinals.

The origin of each is very long, extending along the fibrous aponeurosis between it and the coraco-branchialis and the coraco-arcualis communis, from beneath the origin of the coraco-mandibularis halfway to its insertion on the ventral side of the hyoid copula just behind the lower jaw. The muscle is as thick as broad and only diminishes slightly in size in front.

Raia.

In the skate the coraco-hyoideus muscles (Fig. 3, *Chy*) are reduced, flat, and thin. Each arises from the fascia covering the large coraco-hyomandibularis, near the origin of the second interbranchial muscle and is inserted upon the ventral surface of the hypohyal cartilage. It lies deeper than the depressor rostri, the depressor mandibularis, and the depressor hyomandibularis, and directly upon the coraco-hyomandibularis.

Coraco-branchialis.

Acanthias.

The coraco-branchialis (Figs. 4, 10, *Cbr*) is the deepest and most dorsal of the ventral longitudinal muscles and forms the lateral wall of the pericardial cavity. It is composed of five parts, of which the last four have a common origin. The first division (*Cbr 1*) arises from an aponeurosis directly beneath the coraco-hyoideus, and running dorsally becomes inserted on the dorsal surface of the medial end of the hyal cartilage. It is much shorter than the ceratohyoid and is contracted near its insertion.

The four remaining coraco-branchials (Fig. 10, *Cbr 2-4*) arise from a strong membrane running from the girdle to the origin of the ceratohyoid. As the fibers pass forward and laterally they divide into separate portions, the anterior of which becomes inserted on the branchial arches, while the last, which is much the largest, is inserted upon the fifth arch and upon the lateral half of the copula. Blood vessels pass through the arches between the divisions of the muscle.

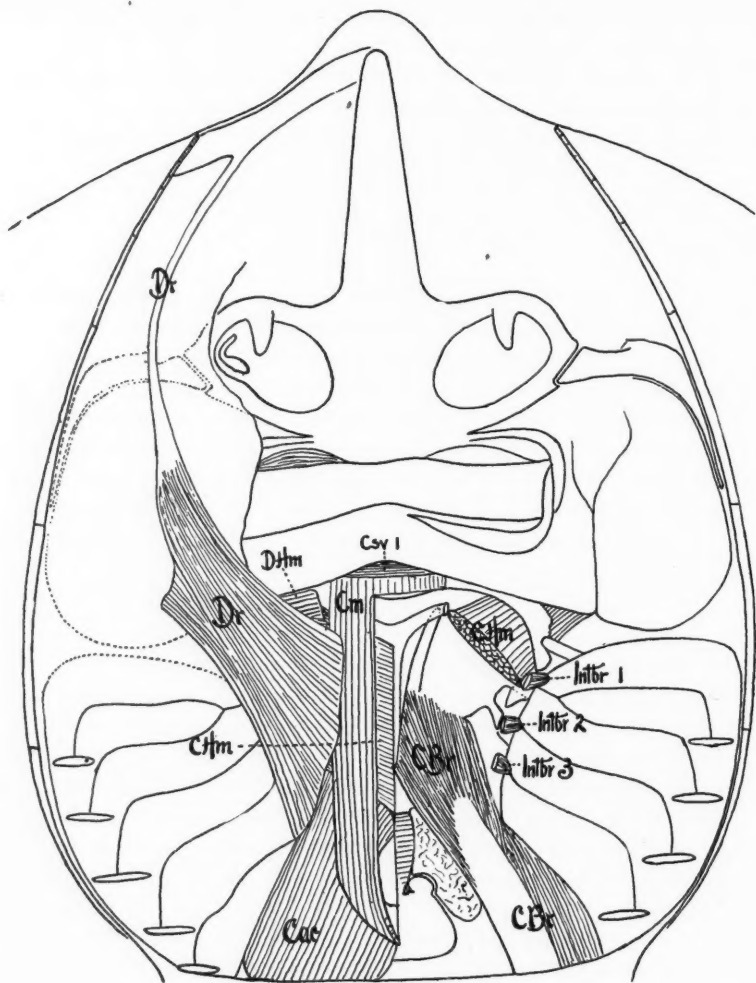


FIG. 15.—Raia, ventral view, after removal of the skin; right half more deeply dissected. *Cac*, coraco-arcualis communis; *CBr*, coraco-branchialis; *CHm*, coraco-hyomandibularis; *Cm*, coraco-mandibularis; *Csy 1*, constrictor superioris ventralis 1; *DHm*, depressor hyomandibularis; *Dr*, depressor rostri; *Intbr 1-3*, interbranchiales.

Raia.

In *Raia* this muscle (Fig. 15, *Cbr*) which forms the lateral wall of the pericardial cavity, arises from the pectoral girdle. Farther forward the muscle expands and the tendon gives place to muscle fibers which are inserted on the anterior process of the basibranchial and the membranous floor of the mouth. The other fibers run dorsally and become attached to the ends of the cerato- and hypobranchials. The divisions between these parts, as in *Acanthias*, permit the passage of blood vessels, and extend nearly back to the origin dividing the muscles into superimposed layers.

Coraco-arcuales communes.

Acanthias.

The paired coraco-arcuales communes muscles (Figs. 4, 5, *Cac*) lie immediately beneath the skin and arise from the coracoid region of the girdle. The fibers run inward and forward, and the medial fibers become inserted in the strong membrane which forms the floor of the pericardium, while the lateral parts are inserted upon the fascia dorsal to the origin of the ceratohyal. Each muscle is crossed by four myosepta, which makes it resemble somewhat the ventral body muscles behind the girdle.

Raia.

In the skate (Figs. 3, 15, *Cac*) this muscle closely resembles that in *Acanthias* in origin, direction, and insertion.

Coraco-hyomandibularis.

This wide, comparatively thick, and long muscle occurs only in *Raia* (Figs. 3, 15, *Chm*) of the forms studied, where it is the largest and most important of the ventral longitudinal muscles. It arises from a fascia in the middle line, and runs forward nearly to the division of the ventral aorta. The muscle runs obliquely

forward and outward, passes the first hypobranchial on the dorsal side, and converges to a small flat tendon on the anterior ventral surface of the hyomandibula.

SUMMARY.

In the foregoing, all of the muscles of the head and the branchial region, with the exception of the eye muscles, have been considered. The two forms studied agree very closely when their difference in shape is considered.

In the skate, as might be expected from its extreme modification, a few muscles are developed which are not found in the dogfish. These are the levator and depressor of the rostrum, and the cerato-hyomandibularis which, from its position, seems adapted to the protrusion of the jaws.

The muscles of the skate referred to by Tiesing as "*Csv* 3-5," are here interpreted as fibers of the interbranchials which have acquired an extreme development.

The muscles in *Acanthias*, marked *Csv* 2 and *Csβ* 2 by Vetter, are here regarded as the first and second ventral constrictors respectively.

The deeper ventral longitudinal muscles of *Raia* are described for the first time.

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OCURRENCE OF *ECHINOSTOMUM SPINULOSUM*
RUD.

N. C. GILBERT.

IN THE intestinal cœca of an adult male Loon (*Gavia imber*) killed near Ann Arbor, Michigan, in April, 1904, I found from forty to fifty mature distomes, which I have identified as *Echinostomum spinulosum* Rudolphi, a worm which I have not been able to find hitherto reported for North America. Later, in August of the same year, I obtained eight more specimens from the intestine of a Bonaparte's Gull (*Larus philadelphia*). In each case the specimens were in a badly macerated condition.

There was this unimportant difference from the European species, that my specimens averaged somewhat smaller. Their length was about 2.37 mm., while the length for the European species is given as from 3-10 mm. (Stossich, '92). The anatomical differences are also very slight between this species and *E. pseudoechinatum* Olsson, *E. euryporum* Loos, *E. mordax* Loos, and *E. pendulum* Loos, and make this species very difficult to differentiate. These differences are, however, very accurately described by Loos ('99), and although slight, seem constant.

The body of the specimens which I obtained is elongated, subcylindrical, widest at the acetabulum, and tapers gradually posteriorly. Length, 2.37 mm.; width at acetabulum, 0.29 mm. The neck is constricted, and is armed with spines, arranged in regular rows, which extend as far as the posterior border of the acetabulum. The anterior end is conical in shape, with an expanded base, and is armed with twenty-two oral spines, in a single row, and of equal size.

The oral sucker is located at the extreme anterior end; diameter, 0.08 mm. The acetabulum is located 0.61 mm. from the anterior end; diameter 0.17 mm. The pharynx is located close behind the oral sucker, and the intestine divides just anterior to

the acetabulum into two cœca of equal length, which extend to the posterior extremity.

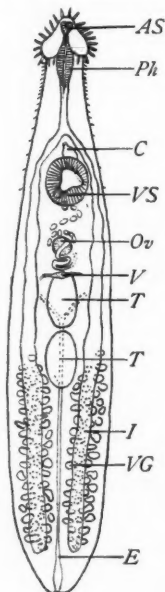


FIG. 1. — *Echinostomum spinulosum*. *as*, anterior sucker; *ph*, pharynx; *c*, cirrus-sac and seminal vesicle; *ov*, ventral sucker; *v*, vitelline receptacle; *t*, testis; *i*, intestine; *vg*, vitelline glands.

The ovary is situated 0.15 mm. back of the acetabulum, in the median line, is round, and is 0.05 mm. in diameter. The oviduct passes posteriorly, makes two simple coils, receives the vitelline duct, and is surrounded by the shell gland. It then passes anteriorly, and after a few turns, it opens to the exterior just anterior to the acetabulum, and beside the cirrus-sac. The ova are rather large, oval, 0.09 by 0.06 mm., and from four or five to twenty-four were counted in one individual.

The vitelline glands consist of a large number of simple follicles, and extend as far anteriorly as the anterior border of the posterior testis. They are scattered over the entire region as far back as the ends of the intestinal cœca, and show a distinct bilateral arrangement. They open by two lateral ducts into a median receptacle, just anterior to the testis.

The testes are oval and relatively large, and located in the same antero-posterior line; length, 0.17 mm. by 0.12 mm., and 0.03 mm. apart.

The cirrus-sac and seminal vesicle lie just beneath the anterior margin of the acetabulum, and open to the exterior a short distance anterior to it.

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